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Effects of Fire Severity and Distance from Unburned Edge on Mammalian Community Post-fire Recovery

Jay Diffendorfer
US Forest Service, jdiffen@uiuc.edu

Wayne Spencer
Wildlife Ecologist Conservation Biology Institute, wdspencer@consbio.org

Scott Tremor
US Forest Service, stremor@sdnhm.org

Jan Beyers
US Forest Service, jbeyers@fs.fed.us

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Principal Investigators: Jay Diffendorfer (217-244-4385; jdiffen@uiuc.edu)
Wayne Spencer (619-296-0164; wdspencer@consbio.org)
Scott Tremor (619-232- 3821 ext. 235; stremor@sdnhm.org)
Jan Beyers (951-680-1527; jbeyers@fs.fed.us)

Other Key Contributors: Genie Fleming, Angelo Soto, Paul Schuette

SUMMARY OF FINDINGS TO DATE

This final report summarizes key findings relative to the five major objectives listed in our proposal, along with the crosswalk of accomplished and future deliverables. Additional details concerning objectives, methods, results, and recommendations are presented in Attachment A.

Each of our major objectives is listed below with a brief summary of findings to date. Because we only recently finished the final session of data collection, all findings are preliminary and may change as more comprehensive statistical analyses are completed.

1. Evaluate the effects of fire on southern California rodent, large mammal, and bat diversity and study patterns of post fire recovery.

Overview: Fire immediately alters the composition of the mammal community in chaparral and coastal sage scrub vegetation, although species responses to fire, including changes over time following fire, are highly species-specific. In chaparral, overall rodent richness is similar between burned and unburned areas, but the composition of the community is very different between these conditions. Furthermore, even after 4 years, the post-burn communities differ from their pre-fire status and from unburned communities. Fire in coastal sage scrub reduced rodent diversity to a simpler community, similar to that that of disturbed habitats dominated by annual grasses and forbs. Carnivore species appear not to be strongly affected by fire. We also detected little effect of burn status on the bat community, although at least two species appear to forage more frequently over unburned chaparral.

Rodents: We examined rodent responses to fire in both chaparral (Cedar Fire; Cleveland National Forest) and coastal sage scrub (Otay Fire; Rancho Jamul Ecological Reserve)

vegetation beginning about 13 months following fire and continuing until 43 months post fire. In both communities we noted substantial differences in mammal community composition between burned and unburned habitat, and in patterns of post-fire responses over time.

Some species were clearly more widespread and abundant in burned than unburned chaparral, others showed the opposite pattern, and still others showed more complex associations with fire over time (Figure 1). For example, the Dulzura kangaroo rat (*Dipodomys simulans*; DISI) was far more common on burned than unburned plots over the nearly 4-year study duration, while the California mouse (*Peromyscus californicus*; PECA) was far more common on unburned plots, and the cactus mouse (*Peromyscus eremicus*; PEER) was equally common on burned and unburned plots.

In unburned chaparral, PECA dominated the rodent community across the entire study period, with several other species varying in their relative abundance over time. For example, the California pocket mouse (*Chaetodiopus californicus*; CHCA) was not abundant on unburned plots during the first spring sampling session, but increased to become the second most abundant species during the last two spring samples (the third and fourth springs following fire). Conversely, the brush mouse (*Peromyscus boylii*; PEBO) was fairly common on unburned plots early in the study, but gradually declined to become a minor component of the community in latter sessions.

Burned plots were dominated by deer mice (*Peromyscus maniculatus*; PEMA) during the first post-fire spring sample, with DISI second most abundant. Over time, PEMA declined in abundance on burned plots, while DISI increased to become the dominant species. The big-eared woodrat (*Neotoma macrotis*; NEMA) was very rare on burned plots although common on unburned plots. In contrast, the desert woodrat (*N. lepida*; NELE) was about equally common on burned and unburned plots.

Despite gradual recovery of some chaparral species on burned plots over time, compositional differences between burned and unburned plots were still pronounced 4 years following fire, and the communities are still changing. Sampling would need to continue for more years to determine when communities return to pre-fire status.

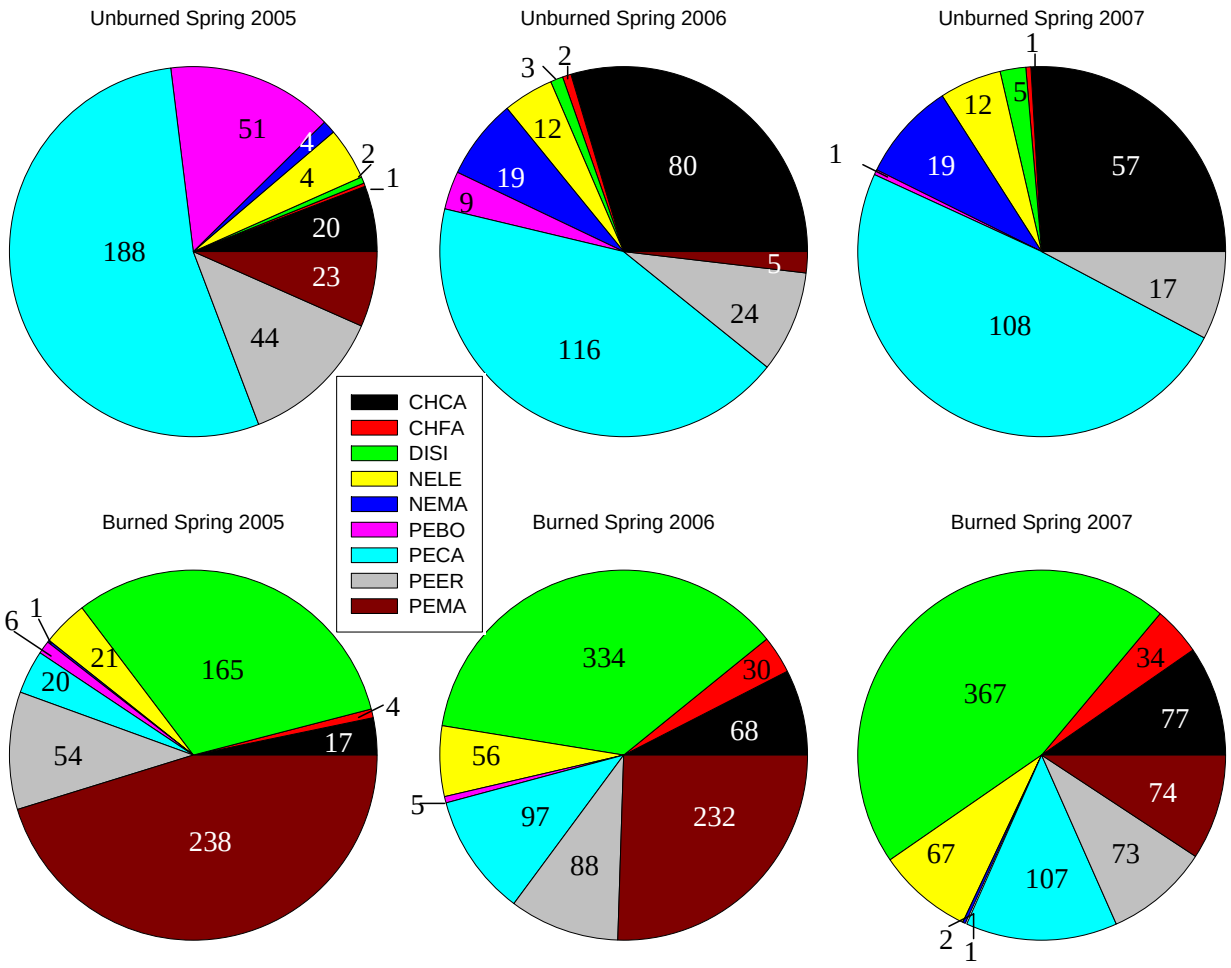

Figure 1. Relative abundance of species during spring trapping sessions in Cleveland National Forest. Abundance was based on minimum number of individuals known alive (numbers) pooled cross all plots within a type. CHCA = *Chaetodipus californicus*, CHFA = *Chaetodipus fallax* , DISI = *Dipodomys simulans*, NELE = *Neotoma lepida*, NEMA = *Neotoma macrotus*, PEBO = *Peromyscus boylii*, PECA = *Peromyscus californicus*, PEER = *Peromyscus eremicus*, PEMA= *Peromyscus maniculatus*.

In coastal sage scrub, fire simplified community composition, resulting in patterns similar to those of disturbed areas dominated by exotic grasses and forbs rather than the more diverse communities observed on undisturbed coastal sage scrub. Moreover, species diversity actually decreased with time following fire in coastal sage scrub, so that by year 4 the rodent community on burned plots was less diverse than either the pre-fire or immediate post-fire sampling periods.

Carnivores. Using a combination of track and camera station surveys throughout burned and unburned areas, we found no evidence that fire affected occupancy patterns or colonization patterns for any species for which we obtained sufficient data (gray fox, *Urocyon cinereoargenteus*; coyotes, *Canis latrans;* and striped skunks, *Mephitis mephitis*). It seems the carnivores we studied were capable of persisting in both unburned and burned chaparral.

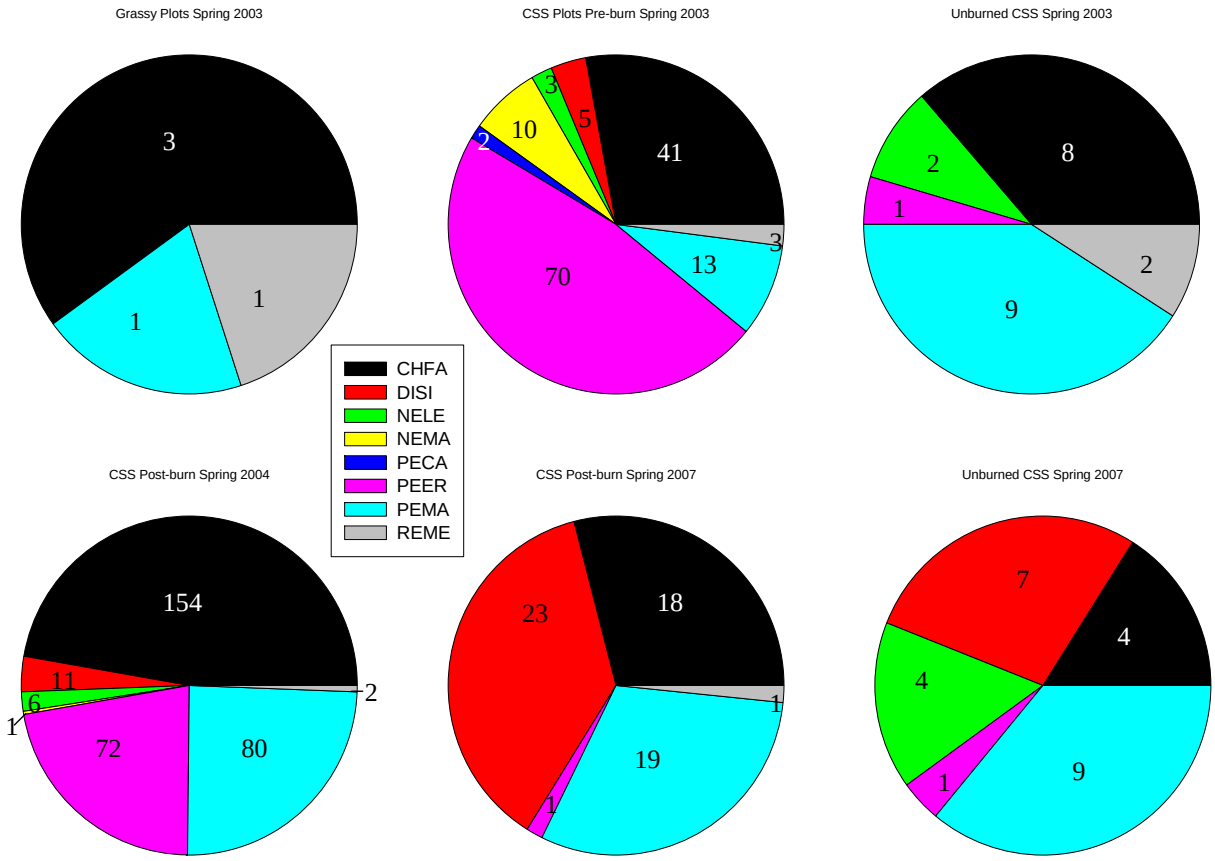

Figure 2. Relative abundance of rodent species during spring trapping sessions on Rancho Jamul Ecological Reserve, based on minimum number of individuals known alive and pooled across all plots within a type. Grassy plots (n = 3) are unburned but dominated by exotic annuals; coastal sage scrub (CSS) plots (n = 9) were burned in 2003; unburned CSS (n = 2) were not burned in 2003. CHFA = *Chaetodipus fallax* , DISI = *Dipodomys simulans*, NELE = *Neotoma lepida*, NEMA = *Neotoma macrotus*, PECA = *Peromyscus californicus*, PEER = *Peromyscus eremicus*, PEMA= *Peromyscus maniculatus*; REME = *Reithrodontomys megalotus*.

Bats. Using automatic-recording ultrasonic bat detectors, we found only small qualitative differences in overall bat diversity between burned and unburned sites. However, activity of two bat species, *Tadarida brasiliensis* and *Myotis californicus*, was higher in unburned habitat.

2. Determine the influence of burn severity on mammal diversity and patterns of recovery.

Overview: Burn severity affects the rodent community via differential effects on post-fire vegetation structure and composition, which in turn affects the distribution, abundance, and recovery trajectory of each rodent species. However, the magnitude of these differences is not great, so that burn severity likely plays a small role in structuring patterns of rodent diversity across space following fires.

Rodents. We limited this analysis to effects on rodents, because fire severity may vary substantially over relatively fine spatial scales relative to the space-use patterns of carnivores and bats. We rated burn severity on rodent plots within the Cedar Fire perimeter using methods described by Keeley (1998. Postfire ecosystem recovery and management: The October 1993

large fire episode in California. Pages 69-90 *in* J.M. Moreno, ed. Large forest fires. Backhuys Publishers, Leiden, Netherlands.). To date we have completed a preliminary examination of whether and how fire severity affected simple patterns of increasing or decreasing abundance following fire, and found a variety of species-specific response (see Attachment A for a detailed summary). Future analysis will consider more complex temporal changes following fire, and will include a variety of other environmental variables, such as soils, elevation, and presence of unburned patches inside the burn perimeter.

Most species responded more directly to vegetation structure and composition following fire than directly to fire severity. However, burn severity did affect vegetation structure and composition, and thus indirectly affected rodent species abundance and rates of change over time to a small degree. For example, higher fire severity plots had slightly higher herb cover than others. California pocket mice responded with higher abundance on plots having higher herb cover (i.e., higher severity on average), and Dulzura kangaroo rats responded with higher rates of population increase on plots having higher herb cover. Conversely, deer mice had lower abundances where herb cover was higher (i.e., lower severity on average). Only one species, California mouse, responded directly to fire severity when we controlled for the effects of differential herb cover and distance from unburned edge (see below). California mouse was more common and had a higher rate of population increase on higher fire severity sites. However, these direct and indirect influences of burn severity on the distribution and abundance of various rodent species were relatively subtle, and probably not important in overall structuring of rodent communities in chaparral, relative to other factors.

3. Determine the role of distance from burn perimeter on diversity and patterns of recovery.

Overview: The large size of the Cedar Fire created an opportunity to investigate the spatial scale over which mammal communities are affected by fire and the pattern of post-fire recovery. Again, rodents responded with species-specific patterns of change over time as a function of distance from unburned edge (Appendix A), which appear in part to reflect differential patterns of post-fire recolonization and population expansion from unburned chaparral versus *in situ* population responses to vegetation change. Surprisingly, carnivore species seemed unaffected by distance from unburned edge. Similarly, bat diversity was not obviously affected by distance to unburned edge.

Rodents: Rodent sampling plots ranged from near the Cedar Fire perimeter (<1km) to ~8km inside the perimeter. We found variable species-specific response to distance from unburned edge. For example, California mice were less abundant in fire interior than edge plots, potentially because this chaparral species recolonizes burn areas progressively from unburned habitat. In contrast, California pocket mouse showed higher rates of increase farther from the edge, and Dulzura kangaroo rat was more abundant farther from the edge. These two species appear to survive fire and respond *in situ* to changes in vegetation structure and composition over time within the burn area, rather than recolonizing from unburned habitat. Why they appear to increase more in burn interior areas than edge areas is unknown based on these preliminary analyses, but could be due to species interactions, whether competition from other "fire edge" species or increased predation closer to the edge. Future multivariate analyses will better

differentiate the relative contributions of distance from unburned habitat and other factors, such as fire severity, species interactions, and vegetation structure.

Carnivores: Distance from burn edge was not a factor in the distribution of any species for which we had sufficient detection data. However, coyotes were found more frequently near residential areas, and more of our plots near the burn edge were close to rural homes. Thus, coyotes *appeared* to occur more frequently near the burn edge, but this apparently reflected their propensity to forage in areas closer to homes more than a propensity to use burn edges. The resulting increased activity of coyotes near homes (i.e., burn edge) may be one factor in why certain rodent prey species (e.g., Dulzura kangaroo rats) were less abundant in fire edge than fire interior sites.

Bats: Though burned sites near the fire perimeter showed qualitatively lower overall bat diversity compared to sites far from the perimeter, differences in bat activity were generally much less pronounced between near and far burn sites than between burned and unburned sites. Because bats are highly mobile relative to the scale of even very large fires, they appear not to differentiate strongly between areas near and far from burn perimeters. However, unburned sites likely provide greater food sources for some species, and we detected many more foraging bats in unburned than burned habitats for at least two species.

4. Use these findings to elucidate future fire intensity levels and perimeter sizes for prescribed fires to support wildlife resource managers.

Overview: Our results suggest that, despite some species-specific effects of fire severity and size (measured as distance from unburned edge), the size and intensity of prescribed fires is unlikely to have significant effects on post-fire mammal communities. Far more important are fire-return intervals and the potential for overly frequent fires to type-convert vegetation, increase invasive exotic plants, and simplify mammal communities by eliminating some species.

Although there were species-specific effects (some indirect) of burn severity and distance from edge on abundance of some rodent species, their magnitude was not great, and the differences appear to decline over time with vegetation succession. The primary effect of severity on rodent species appeared to be its effect on herb cover. There were no apparent effects of severity or distance from edge on either carnivores or bats.

The Cedar fire was far larger than what is logistically feasible for prescribed burns, and it seems unlikely that size of prescribed burns will have biologically significant effects on small mammals, except perhaps in certain situations (e.g., presence of rare or endangered species in fragmented habitat areas). The distances over which we recorded differential effects in post-fire mammal recovery (e.g., faster recovery of California mice near unburned habitat than several kilometers away) seems biologically insignificant at the scale most prescribed burns are performed. Likewise, prescribed fires are usually restricted to conditions when extreme burn severity is unlikely, so the relatively subtle effects of severity on rodent species and communities we observed are not a great concern.

The relationship we found between fire severity and herb cover, though small, may be of some importance, as it is mainly driven by the cover of exotic species. If high fire severity, as opposed

to some other factor, facilitates increases or persistence of exotic annuals, this could affect mammal communities over space and time. Our results in burned chaparral sites show some mammal species do well where herbs, including exotics, are higher following fire. However, herb cover was relatively low, particularly 3-4 years following the Cedar Fire. In contrast, herb cover, particularly of exotic species, was very high on burned coastal sage scrub plots (Otay Fire), and the simplified mammal community we observed there appears not to be recovering over time, and indeed declined in diversity in the years following the fire. More years of field data collection, and further multivariate analyses, are needed to elucidate the longer-term effects of fire on post-fire recovery and to elucidate the relative effects of site-specific factors versus fire size and severity.

Small mammal communities are likely strongly structured by bottom up effects driven by the composition, successional stage, structure, and level of invasion in the vegetation community. In all cases, the largest changes in mammal communities came when comparing burned to unburned plots. Furthermore, such contrasts often resembled comparisons between degraded plots having high levels of exotic species and plots with intact shrub communities.

Fire impacts on small mammals and bat communities are mediated through fire impacts to vegetation. This suggests management that maintains chaparral and coastal sage scrub vegetation communities in the face of increased fire return intervals and exotic invasion will also be the most effective means of maintaining intact mammal communities. Thus, managing fire return intervals, type conversion, and the scale of patchiness in burned, unburned, and recovering vegetation across large landscapes is more important than controlling fire size or severity. Burn size and intensity play a roll, not in how they immediately impact mammals, but in how they impact these landscape-level attributes.

Further complicating the management scenario is climate change, which is predicted to increase drought in southern California. Increased dryness and prolonged fire seasons will likely favor more fires, but it will also impact post-fire recovery. Lack of rainfall will likely hamper population growth for many small mammals and perhaps constrain carnivores to areas having perennial water sources. Furthermore, because drought differentially affects exotic grasses and native shrubs, the vegetation community may be less likely to recover if droughts follow fire.

5. **Disseminate these results using reports, journal articles, public presentations, web pages, and the San Diego County Mammal Atlas being prepared by the PI's in collaboration with others**.

Deliverables Crosswalk

The following table summarizes all deliverables listed in our proposal and which have been completed or are to be completed in the future, as well as some deliverables not in our proposal also completed under funding provided by this grant.

Proposed	Delivered	Status
[1]Annual Progress Reports		done
[1]Presentations	1. California Department of Fish and Game, San Diego, CA, March 20, 2006 2. United States Fish and Wildlife Service, Carlsbad, CA, 3. San Diego Partners for Biodiversity. 4. Society for Conservation Biology meeting in San Jose, CA, in June 2006 5. 3rd International Fire Ecology and Management Conference, San Diego, CA, November 13-17, 2006 6. Defenders of Wildlife Sixth Annual Carnivore Conservation Conference, St. Petersburg, Florida, November 2006 7. Poster presented at 2nd Fire Behavior and Fuels Conference, March 26-30, 2007, Destin, FL.	1. done 2. done 3. scheduled 4. done 5. done 6. done 7. done
Submission of at least one manuscript on patterns of recovery across burn severity and distance from burn perimeter upon completion of studies	1. Carnivore habitat use after a large wildlife in Southern California. 2. Does vegetation, burn intensity, and distance to unburned habitat influence patterns of small mammal community recovery from wildfire? 3. Bat community response to wildfire	1. Reanalysis of P. Schuette thesis complete. Revising thesis for publication. 2. Analyses underway. 3. Done. More analyses will follow for publications.
Database	A linkable database for vegetation, small mammals, bats, and carnivores that is suitable for analyses.	Done

[1] Powerpoint presentations, posters, abstracts of presentations, and progress reports will be included on the CD being mailed to the JFSP with the final report.

Proposed	Delivered	Status
A chapter in the upcoming book "The Mammals of San Diego County," edited by the PI's		In process
Annual production of GIS map layers delivered to various local agencies and made available on the San Diego Mammal Atlas web page and other appropriate web pages.		In process
Website[2]	http://www.sdnhm.org/research/postfire/index.html	Done
Final report	This document	Done
Masters thesis (not initially proposed)	Paul Schuette. San Diego State University. "Carnivore community response to a large wildfire in San Diego County, California"	Done

[2] The website should be online beginning October 8, 2007.

ATTACHMENT A

Preliminary analysis of small mammal abundance following fire in chaparral

Fire can dramatically affect the collection of species, and the abundance of each species, within a burn area; and such fire attributes as severity and size may affect how the community and species populations are impacted by the fire and recover following the fire. We examined differences in community composition and individual species abundance for small mammals (rodents) following the October 2003 Cedar Fire in San Diego County, California. Given the immense size and variability of the Cedar Fire, it represented a unique opportunity to explore how factors like fire size and severity affect patterns of post-fire recovery. We systematically sampled the distribution and abundance of chaparral-associated rodent species at varying distances inside the Cedar Fire perimeter, and in areas of varying burn severity. We also sampled in unburned chaparral vegetation outside of the fire perimeter. Finally, we measured vegetation and other environmental attributes at all sample plots, because how fire and post-fire succession change vegetation attributes is likely to have a strong "bottom-up," resource-based influence on rodent populations.

In this preliminary analysis of post-fire rodent communities, we examined only simple trends of increasing or decreasing individual species abundance over time to determine patterns of post-fire recovery in a very general sense. Four general patterns were anticipated. First, a species abundant on unburned plots might start with low abundance on burned plots but gradually increase over time, suggesting progressive recovery. Second, a species might be equally abundant through time on burned and unburned plots, suggesting little initial effect of fire or very rapid recovery. Third, a species might be abundant on unburned plots but show low abundance through time on burned plots, suggesting slow or poor recovery. Finally, a species might be initially abundant on burned plots and show gradual declines over time while remaining generally low on unburned plots, suggesting the species favors the early post-fire environment and declines as the vegetation recovers.

While these simple linear trends in abundance over time are informative, more complex nonlinear temporal trends are possible and may result from factors including, for example, competitive interactions between species and inter-annual climate trends. We will examine such interactions and additional factors in future analyses. These initial analyses have helped elucidate where more complex analyses are warranted.

Methods

We established 10 unburned and 30 burned plots, spaced at least 300m apart, in chaparral habitat within Cleveland National Forest. Burned plots spanned a range of fire severities and distance inside the Cedar Fire perimeter. Fire severity was measured in the field using index values described in Keeley (1998). Distance was measured as the shortest distance, in kilometers, between the plot center and the fire perimeter. Burned plots were located <1km to ~8km inside the perimeter. Unburned plots were within 2km of the burned area, in areas having the similar chaparral vegetation as on burned plots (dominant shrub species were chamise, scrub oak, and manzanita). Plots were roughly 100m by 20m and included two rodent trapping lines and two vegetation sampling lines to the outside of each trap line. Vegetation was surveyed in spring and rodents were surveyed spring and fall each year on each plot over a roughly 2.5-year period,

beginning ~13 months after the fire (November 2004) and extending until 43 months post-fire (May 2007).

Vegetation

Each plot included two 100m x 1m belt transects for vegetation sampling, located ~5m to the outside of each small mammal trap line. Vegetation was sampled each spring when plants were at or near their phenological peak. Burned plots were sampled in 2005, 2006, and 2007. Unburned plots were sampled in 2005 and 2007 only to reduce damage to vegetation due to the physical difficulty of moving through mature chaparral.

At each sample we estimated the canopy cover and maximum height of woody species and herbs across the plot using a point intercept method. Fifty sample points were spaced at 2m intervals along each transect starting at 0.5m. We recorded the identity and maximum height, to the nearest 0.1m, of each species intercepting each point. Canopy cover was calculated as the number of points where a particular type of vegetation was recorded, divided by the total number of sample points. Separate calculations were made for woody species, all herbs, nonnative herbs, native annual herbs, and native perennial herbs.

Ten $1m^2$ quadrats were located at 10m intervals along each transect. We measured the height and status (live [>0.2m tall], dead, killed by fire, resprout, seedling [<0.2m tall]) of all woody species rooted within each quadrat. Woody species included shrubs, subshrubs, and suffrutescents with generally persistent shrub-like canopies. We then calculated density of woody species in $20m^2$ as the total number of individuals counted within each status in all 20 quadrats combined. Pre-fire density of shrubs was estimated as the average number of killed and resprouting individuals counted in $20m^2$ in 2005 and 2006 combined.

Within each quadrat we also measured two finer-scale vegetation properties, which we thought might influence small mammals: basal vegetation and visual obscurity. Basal vegetation was visually estimated as the percent of the quadrat covered by any vegetation (live, standing dead, litter) within 10cm of the ground surface. This variable may reflect ease of movement and foraging for some species. Obscurity was visually estimated as the percent of a vertically oriented meter-stick obscured by vegetation. Separate obscurity estimates were made within 3 height classes: 0 - 0.3m, 0.3-0.6m, and 0.6-1.0 m from the ground surface. Obscurity may, like basal vegetation, affect foraging, but it also may be indicative of cover and, hence, risk of predation.

During the first post-fire spring, we measured the diameter of the smallest remaining stem on 40 burned chamise (*Adenostoma fasciculatum*) skeletons. Using the 20 $1m^2$ quadrats on each plots as focal points, we measured the two skeletons closest to the center of each quadrat. Each stem diameter was converted into a fire severity index value following Keeley (1998), and the mean index value per plot was used. Index values were chosen over actual stem diameters because the most severely burned plot (with a large median stem diameter) often appeared as an influential outlier in preliminary analyses. Use of index values reduced the influence of this single plot on statistical tests.

Mammals

Rodents were sampled twice per year (spring and fall) during 5-night trap sessions. We used 30 baited Sherman XLK folding traps in two lines, 15m apart, with 7m intra-line spacing. We baited traps before dusk with roasted (to prevent germination) sunflower seeds and checked traps the following morning for 5 consecutive mornings. For each animal captured we assigned a

unique marker and recorded date, trap location, species, weight, gender, age, and reproductive characteristics. Small mammal abundance within each species and trapping session was subsequently calculated as the minimum number known alive (MNKA) based on captures from successive trapping sessions.

Statistical Analyses

Repeated sampling of plots allowed us to investigate how vegetation structure and small mammal species abundance changed over time within plots. We were also able to evaluate whether variation among plots in change over time, as well as differences in average structure or abundance at specific time points, was related to burn condition (burned vs. unburned), fire severity, or distance from the burn perimeter.

Vegetation

We used either repeated measures analysis of variance (rmANOVA) or hierarchical linear models (HLM; see Appendix 1) to statistically test trends over time and factors influencing those trends. RmANOVA was used when comparing changes over time in vegetation on burned versus unburned plots. In these cases, only the 2005 and 2007 samples from burned plots were utilized for consistency between burn conditions. Differences in the vegetation trends over time between burned and unburned plots were tested using linear interaction contrasts (Time*Burn). Significant interactions were followed up with paired sample t-tests within each burn condition to test change over time and independent samples t-tests within each year, with degrees of freedom adjusted for unequal variances, to test differences between burned and unburned plots.

HLM was used for all other tests of change over time because the procedure is more flexible and statistically efficient than rmANOVA when sufficient data are available. In brief, HLM employs a multi-level, mixed-effects model structure to allow regression-style analysis of data with a nested, or hierarchical, structure such as the sampling sessions nested within plots structure of our study. HLM allowed the simultaneous testing of (a) whether there was an average trend over time across all plots in vegetation structure; (b) whether the trend over time differed as a function of burn condition, fire severity, or distance to the burn perimeter; and (c) whether within-year average vegetation structure differed as a function of burn condition, fire severity, or distance.

With respect to within-year differences, HLM specifically tests such differences at only one time point, defined by the scaling of the time variable (see Appendix 1). In analyses of vegetation, we tested differences either at the first (spring 2005) or second (spring 2006) vegetation sample. Vegetation cover was generally high during the first spring sample as rain was abundant that growing season. However, the second sample (i.e., the mid-point) was chosen as test point when nonlinear vegetation trends were seen due the necessity of time variable centering (i.e., repositioning the relative location of zero values). Nonlinear trends were tested using polynomial variables for time (i.e., time and time^2), and time was centered around the midpoint to reduce nonessential multicollinearity between the time polynomials. Unlike small mammal abundance, nonlinear trends in vegetation were examined because weather patterns following fire (a wet year followed by two dry years) often resulted in clear, easily explainable quadratic patterns.

Rodents

We compared small mammal community composition between burned and unburned plots and through time using relative species occupancy and relative species abundance. For each spring sample, the number of plots occupied by each species in each burn condition was tabulated based on MNKA. Abundance by species was also summed over all plots within each burn condition, and relative abundance was calculated as the percent of the total number of animals.

Where possible, we examined trends in individual species abundance statistically using HLM. We examined whether trends, or within-year differences, varied based on burn condition, fire severity, and distance to the fire perimeter. We also examined the influence of vegetation structure. We used only two vegetation variables, (1) woody species cover and (2) total herb cover (ignoring origin), because they were related to fire severity or distance and likely responsible for similar relations seen among other vegetation variables (see Results). With respect to vegetation influences, we were interested in examining whether general (vs. year-specific) differences in woody or herbaceous cover among plots influenced trends over time or within-year average abundance. Because woody cover and herb cover in 2005 were positively correlated with future values, we used 2005 cover values as an index of each plot's woody cover or herb cover. While woody and herbaceous cover can often be highly negatively correlated, the correlations within our data were moderate and did not prevent entering the two variables simultaneously into statistical models. Because small mammal abundances on burned plots were often very low at the start of the study, but increased over time, within-year differences in average abundance were explicitly tested in HLM models at the study midpoint (i.e., 28 months since fire).

Variable transformations

Throughout our analyses, dependent variables with heavily right-skewed distributions were often started-log transformed (ln[x+1]). Transformations were driven by the distribution of residuals from initial analyses and used as necessary to meet the assumptions of statistical tests. Transformed variables included woody species densities, nonnative herb cover, native annual and perennial herb cover, and abundance of all small mammals. Where log transformations were used, resulting statistical coefficients are typically described in terms of the percent or factor (rather than raw unit) change in variables. Graphic displays of such variables are presented in the original (untransformed) metric, for easier interpretation, based on back-transformation of means, confidence intervals, or expected values.

Results

General trends in vegetation structure by burn condition

Trends in canopy cover and maximum canopy height of woody plants differed based on burn condition (*Cover*: rmANOVA Time*Burn, $F_{1,38} = 34.1$, $p < 0.001$; *Height*: Time*Burn, $F_{1,38} = 6.7$, $p = 0.014$; Figure 1a). Woody cover (live and dead) and average maximum canopy height were consistently higher on unburned plots (*Cover*: 2005 mean difference = 42.5, $t_{38} = 11.2$, $p<0.001$; 2007 mean difference = 24.5, $t_{38} = 8.7$, $p<0.001$; *Height*: 2005 mean difference = 0.92m, $t_{38} = 14.8$, $p<0.001$; 2007 mean difference = 0.86m, $t_{38} = 14.2$, $p<0.001$). However, percent woody cover decreased slightly over time on unburned plots (mean change = 2 units, $t_9 = 3.19$, $p = 0.01$), while canopy height was relatively stable. On burned plots, cover increased by

16 units and height increased by 0.1m over the two year period examined (*Cover*: t_{29} = 9.07, p<0.001; *Height*: t_{29} = 9.77, p<0.001).

Changes over time in woody species density also varied by burn status (Time*Burn, $F_{1,38}$ = 34.08, p <0.001 Figure 1b). The number of live adults in 20m^2 was much higher on burned plots than on unburned (*2005*: average burned density = 2*unburned, $t_{21.9}$ = 9.54, p<0.001; *2007*: average burned density = 4*unburned, $t_{25.5}$ = 16.23, p<0.001) and increased on burned plots by an average of 65%, from 2005 to 2007 (t_{29} = 10.56, p<0.001) but showed little change on unburned plots. Woody species seedling densities were ~9 times higher on burned than unburned plots (Burn main effect: $F_{1,38}$ = 49.53, p<0.001; Figure 1c) but declined by an average of 56% over time in both burn conditions (Time main effect: $F_{1,38}$ = 47.35, p<0.001). While seedling declines on both burned and unburned plots likely result from mortality and germination failure due to adult shading and drought, declines on burn plots likely also include "losses" due to transitions to the adult stage, contributing to the increase in adult density seen on burned plots.

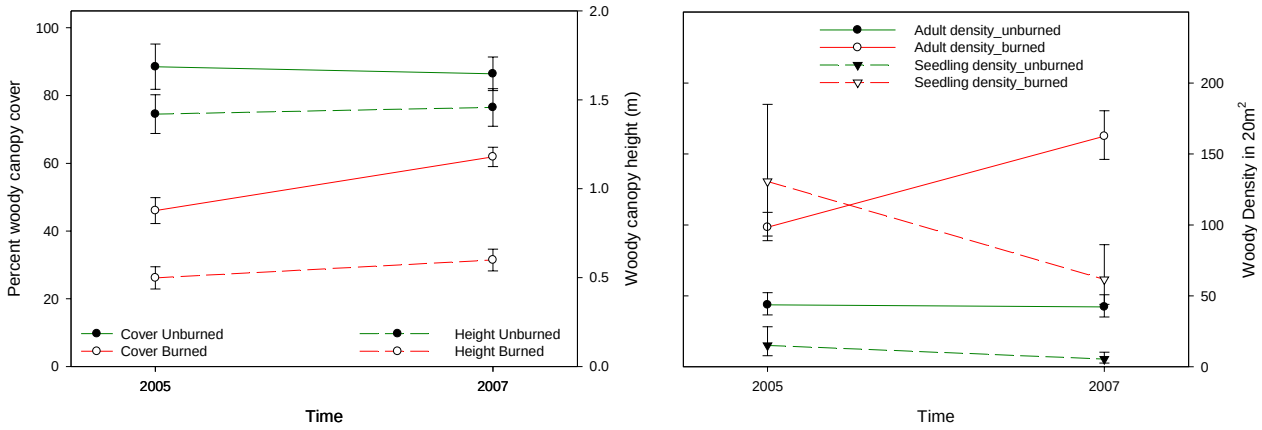

Figure 1. Woody species canopy cover, height, and density. (a) Percent woody cover (left axis, solid lines) and maximum canopy height (right axis, dashed lines) on burned (red) and unburned (green) chaparral plots. (b) Density in 20m2 of woody species adults (solid lines) and seedlings (dashed lines). In all cases bars represent 95% confidence intervals. Average density and confidence intervals are based on back-transformation of log values.

Trends in herb cover (grasses and forbs) varied according to burn status (*Cover*: Time*Burn, $F_{1,38}$ = 30.5, p <0.001). Percent herb cover was 24 units higher on burned than unburned plots in 2005 (t_{38} = 4.6, p < 0.001), but declined over time in both burn conditions likely due to low rainfall in 2006 and 2007 (Figure 2a). Declines were steeper on burned plots and differences based on burn status were no longer significant in 2007 (*Unburned*: mean change = -21.4, t_9 = 5.48, p<0.001; *Burned*: mean change = -42.8, t_{29} = 23.4, p<0.001).

Similar to the trend in total herb cover, cover of native annual herbs was highest on burned plots in 2005 ($t_{9.5}$ = 3.7, p = 0.004), but also declined most on burned plots so that native annual cover was similarly low among all plots in 2007 (Figure 2b; Time*Burn, $F_{1,38}$ = 6.0, p = 0.019; *Unburned*: mean loss = 86% of 2005 value, t_9 = 6.95, p<0.001; *Burned*: mean loss = 96% of 2005 value, t_{29} = 38.03, p<0.001). Cover of nonnative herbs, which were all annual, was relatively low on all plots in all years, but the ratio of nonnative annuals to native annuals increased by a factor of 4 on burned plots only (Time*Burn, $F_{1,38}$ = 5.20, p = 0.001; *Burned change*: t_{29} = 38.03, p<0.001). On unburned plots, nonnative and native annuals had similar

cover and declined at similar rates so the nonnative/native ratio remained relatively constant. However, nonnative cover showed less decline on burned plots compared to unburned (Time*Burn, $F_{1,38} = 7.62$, $p = 0.009$; *Unburned*: mean loss = 82% of 2005 value, $t_9 = 5.18$, $p = 0.001$; *Burned*: mean loss = 54% of 2005 value, $t_{29} = 4.52$, $p<0.001$) and was slightly higher than native annual cover on burned plots in 2007 (Figure 2b; paired t-test, exotic cover = 3*native annual cover, $t_{29} = 7.05$, $p<0.001$). Perennial herb cover (all native) showed a slight decline over time on burned plots only (Time*Burn, $F_{1,38} = 6.51$, $p = 0.015$; *Burned*: mean loss = 55% of 2005 value, $t_{29} = 6.27$, $p<0.001$), but differences between burn conditions were small in both years (Figure 2c).

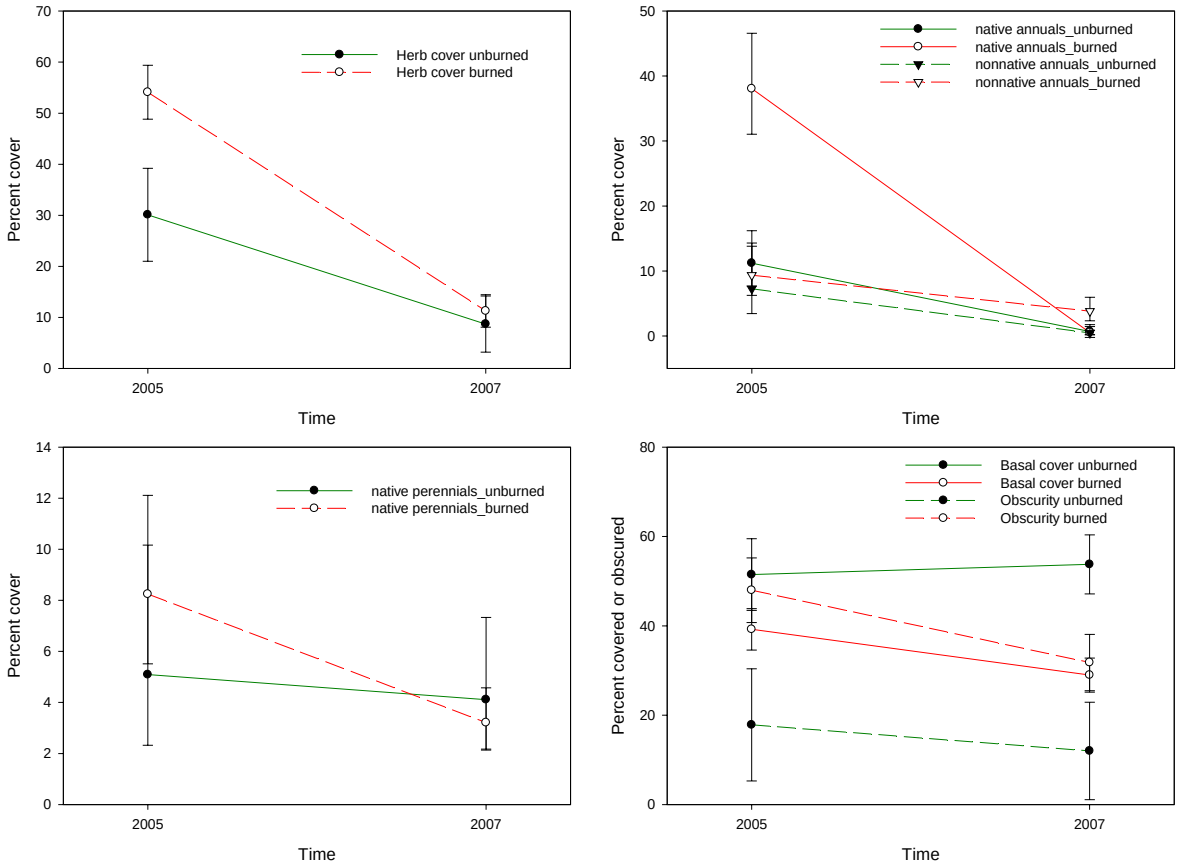

Figure 2. Herbaceous canopy cover. (a) Total percent herb cover on burned (red) and unburned (green) chaparral plots. (b) Percent cover of native (solid lines) and nonnative (dashed lines) annual herbs. (c) Percent cover of native perennial herbs. (d) Percent basal vegetation cover in 1m2 (solid lines) and percent visual obscurity within 0.3m of the ground (dashed lines). In all cases bars represent 95% confidence intervals. Averages and confidence intervals for native annuals, nonnative annuals, and native perennials are based on back-transformation of log values.

Fine-scale vegetation properties (percent basal vegetation cover in $1m^2$ and visual obscurity) also showed differences between burned and unburned plots (Figure 2d). Percent basal vegetation (PBV) did not differ significantly between burn conditions in 2005, averaging 45%, but through 2007 PBV remained relatively constant over time on burned plots while declining an average of 10 units on burned plots (Time*Burn, $F_{1,38} = 12.49$, $p = 0.001$; *Burned change*: $t_{29} = 7.50$, $p<0.001$). In 2007, PBV on burned plots was an average 24 units lower than

on unburned plots ($t_{9.9}$ = 4.39, p= 0.001). These patterns likely result from the substantial drop in herb cover, especially native annuals, on burned plots, whereas basal cover on unburned plots was more consistently composed of shrub bases and litter cover. Visual obscurity within 0.3m of the ground showed different patterns than basal vegetation. Obscurity to 0.3m was an average of 24 units higher on burned plots throughout the study period (Burn main effect, $F_{1,38}$ = 20.85, p < 0.001) and showed a similar decline in both burn conditions, averaging a loss of 11 units between 2005 and 2007 (Time main effect, $F_{1,38}$ = 8.08, p = 0.007). These differences likely result from the low influence of litter cover on vertical obscurity measures relative to basal vegetation measures. Among burned plots, visual obscurity measures for heights above 0.3m (0.3-0.6m and 0.6-1.0m) were mostly at or near zero, and there was little evidence of an increase over time. In contrast, visual obscurity within upper height classes on unburned plots averaged ~20% in each class, but also showed little change over time.

Influence of fire severity and distance on vegetation trends

Fire severity on our plots was negatively correlated with estimated pre-fire density of woody species and the number of killed shrubs (*pre-fire density*: Spearman's rho = -0.54 p = 0.002; *killed density*: Spearman's rho = -0.46, p = 0.01) and was unrelated to the ratio of killed shrubs to resprouting shrubs (where a high ratio could indicate higher mortality among individuals present before the fire). This is contrary to what might be expected, because higher shrub densities might be expected to provide more (or more continuous) fuel and, thus, contribute to higher fire severity and higher shrub mortality. However, our findings may be biased by underestimation of pre-fire density and mortality due the difficulty of detecting burned shrub skeletons that may have been completely consumed above-ground on high fire severity plots.

Among burned plots, post-fire density of live adult woody species in $20m^2$ (resprouts and post-fire recruits combined) showed little relation to fire severity or distance from perimeter, even though pre-fire shrub density was positively correlated with distance (Spearman's rho = 0.46, p = 0.01). While adult density showed an overall increase between 2005 and 2007, as noted in comparison with unburned plots, the greatest increase occurred between 2005 and 2006 followed by a slight decrease through 2007 (Figure 3a; see Appendix 2 Table 1 for statistical details).

In contrast to adult density, woody seedling density decreased relatively steadily through the study period, but starting densities in 2005 and the subsequent rate of decrease were higher closer to the burn perimeter (Figure 3b; Appendix Table 1). 2005 seedling density decreased by 9% with each additional kilometer away from the burn perimeter, so the rate of decline over time increased with distance since seedling densities were similarly low across all burned plots in 2007. Increased seedling density closer to the burn perimeter could suggest nearby unburned areas provide a seed source and, thus, the possibility of slower shrub recovery on interior sites when fire sizes a large. Since post–fire adult densities did not increase with distance, despite higher pre-fire densities on interior sites, slower recovery relative to pre-fire conditions is a possibility on our study sites. However, because post fire adult densities were well above estimated pre-fire densities (paired samples t-test, t_{29} = 10.5, p<0.001) and those seen on unburned sites, slow recovery on interior sites is not an immediate concern.

Changes in woody cover were not constant over the 3-year study period on burned plots. Most of the increase between 2005 and 2007 occurred between 2005 and 2006, then cover remained relatively constant (Figure 3c; Appendix 2 Table 2). While trends over time did not

vary significantly among plots, percent woody cover was higher on plots farther from the fire perimeter, increasing by 1.3 units on average with each kilometer away from fire perimeter. This relationship between distance and woody cover may be driven, at least in part, by high *Lotus scoparius* (deerweed) cover on many mid to interior sites. This subshrub often had a large, round, dense canopy in 2005 and later years, and its cover was positively correlated with distance in 2005 and 2006 (Spearman's rho = 0.41-0.46, $p \leq 0.022$). Woody cover showed little relation to fire severity, but mean maximum woody canopy height increased with fire severity in 2005 (Appendix 2 Table 2). All plots showed a similar rate of height increases over time, so the height difference with fire severity remained relatively constant through the study period. This relationship between woody canopy height and fire severity is probably driven by *Quercus berberidifolia* (scrub oak). Across all burn plots, scrub oak was among the tallest woody species and its cover was positively correlated with fire severity in all years (Spearman's rho = 0.51-0.57, $p \leq 0.004$). Because scrub oak is a strong resprouter, post-fire cover is probably positively related to pre-fire cover. High pre-fire cover of scrub oak likely contributes to high fire severity since scrub oak canopies are typically large with many thick stems and a dense litter layer underneath.

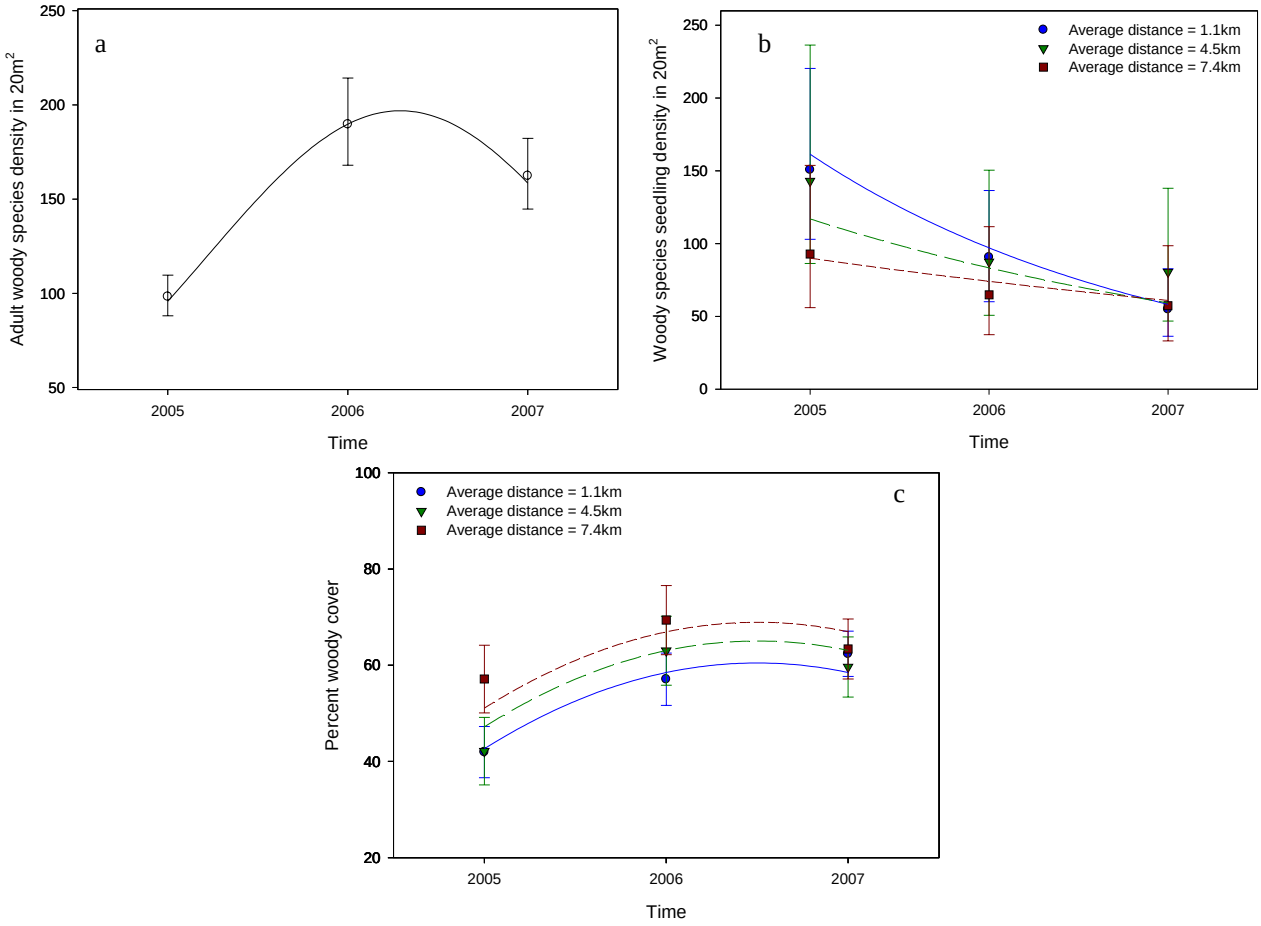

Figure 3. Woody species density and cover over time and as a function of distance from the fire perimeter. (a) Density of woody species adults in $20m^2$. (b) Density of woody seedlings in $20m^2$. (c) Percent woody cover. In all cases, points represent within-year and within distance class (graphs b and c) averages; bars represent 95%

confidence intervals for the averages; and curves represent expected values based on statistical models. Average density of adults and seedlings and their confidence intervals are based on back-transformation of the log values. Note that points and their intervals are shown primarily to give the viewer a sense of the location and spread of data within each class, rather than as formal tests of differences in the means. In graphs b and c, average density or cover may not appear to differ significantly among distance classes because they are based on categorization of a continuous variable and, thus, are not highly distinct groupings. However, models supported an incremental change in density or cover with an incremental change in distance.

Similar to woody cover, declines in total herbaceous cover were greatest between 2005 and 2006, though declines continued at a lesser rate through 2007. Trends over time did not vary substantially among burn plots, but within-year herb cover varied as a function of both fire severity and distance (Figure 4a and b; Appendix 2 Table 3). Percent herb cover increased by 3.5 units for every 1 unit increase in fire severity and decreased by 1.54 units for every kilometer away from the fire perimeter. Distance alone explained greater proportional variance in within-year herb cover compared to fire severity alone (0.24 vs. 0.11), indicating it was the stronger effect though this is likely related to the greater range cover by distance values.

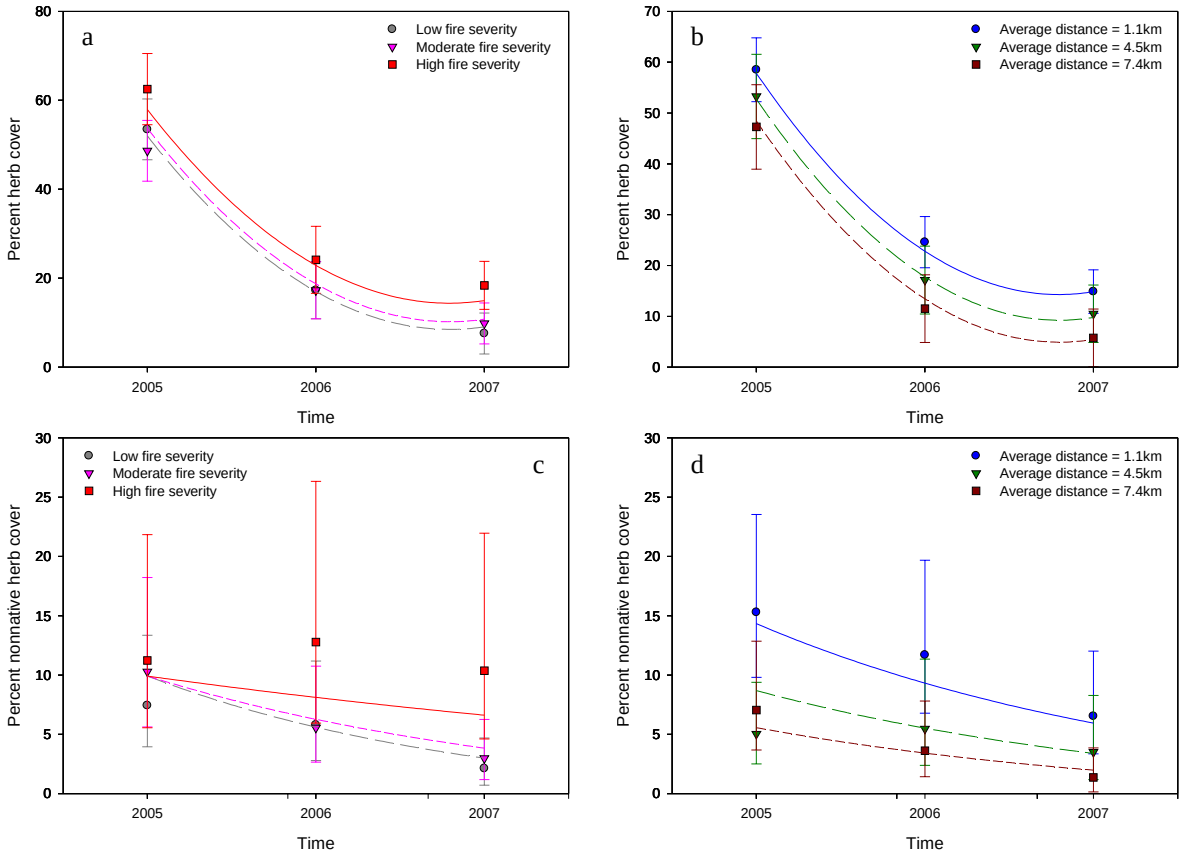

Figure 4. Herbaceous cover over time and as a function of distance from the fire perimeter and fire severity. (a) Percent total herb cover by fire severity class. (b) Percent total herb cover by distance class. (c) Percent nonnative herb cover by fire severity class. d) Percent nonnative herb cover by distance class. In all cases, points represent within-year and within-class averages, and bars represent 95% confidence intervals for the averages. Curves represent expected values based on statistical models, holding other variables in the model constant at their means. Nonnative cover and its confidence intervals are based on back-transformation of log values. As in Figure 4, average

cover does not necessarily differ significantly among distance or fire severity classes because they are not highly distinct groupings. However, models supported an incremental change in cover or its slope over time with an incremental change in distance or fire severity.

Regardless of their relative strengths, both fire severity and distance effects on herb cover may be largely driven by annual herb cover, especially nonnative cover in the last two sample years. Nonnative herb cover did not significantly vary as a function of fire severity in 2005, but the subsequent rate of decline was lower on higher severity sites (Figure 4c; Appendix 2 Table 4). This would contribute to differences in the within year total herb cover with fire severity noted above in 2006 and 2007. Similarly, nonnative cover was lower on plots farther from the burn perimeter in 2005 (Figure 4d; Appendix 2 Table 4) contributing to the distance effect on total herb cover. Native annual herb cover showed similar patterns, but differences in native annual cover were much less pronounced in the later years (Figure 5 a and b). Also, the fire severity and distance effects on native annual cover were weaker than on nonnative cover both in terms of variance explained and the differences implied by the coefficients (Appendix 2 Table 5). For example, exotic cover decreased by 12% for every 1km away from the fire perimeter, while native cover decreased by 4%. Nonetheless, fire severity and distance showed little influence on the ratio of nonnative herb cover to native annual cover. Native perennial herb cover also showed little relation to fire severity or distance (Appendix 2 Table 5).

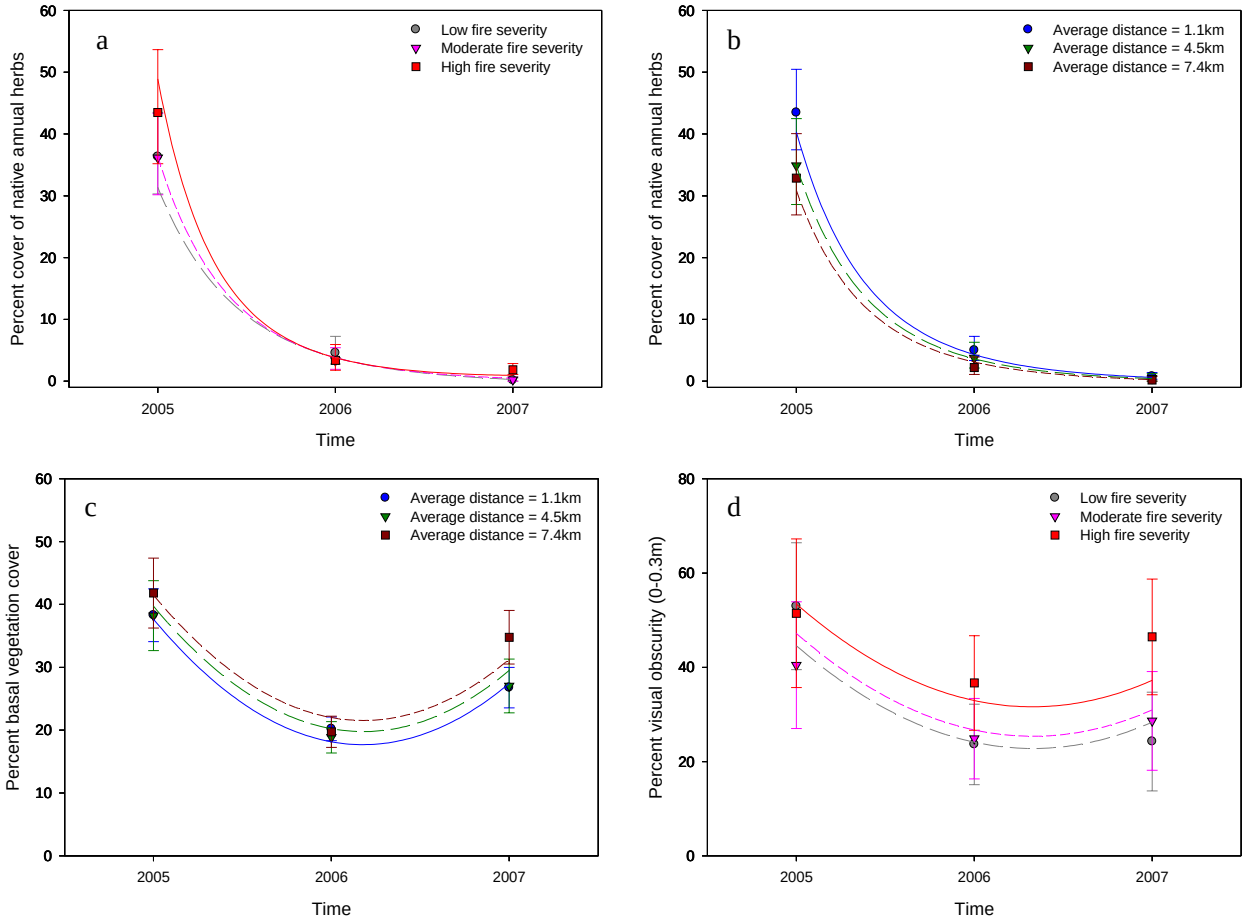

Figure 5. Cover over time and as a function of distance from the fire perimeter and fire severity. (a) Percent native annual herb cover by fire severity class. (b) Percent native annual herb cover by distance class. (c) Percent basal vegetation by distance class. d) Percent visual obscurity from 0-0.3m by fire severity class. In all cases, points represent within-year and within-class averages, and bars represent 95% confidence intervals for the averages. Curves represent expected values based on statistical models, holding other variables in the model constant at their means. Native annual cover and its confidence intervals are based on back-transformation of log values. Although average cover does not necessarily differ significantly among distance or fire severity classes, models supported an incremental change in cover or its slope over time with an incremental change in distance or fire severity.

Distance effects on annual herb cover likely arise from higher woody cover on more interior sites, as described above. Woody cover and annual herb cover are often negatively related since dense shrub canopies can shade out annuals. The positive fire severity effect on herb cover is more difficult to explain since severity did not have an obvious corresponding negative influence on woody cover. A more detailed investigation of herb species composition may be required to explain the effect, but at very least it suggests high severity fires in and of themselves do not dampen cover of native or exotic annuals in the post-fire environment.

As with other forms of vegetation cover, declines in average percent basal vegetation in $1m^2$ were not constant through time. Declines were greatest between 2005 and 2006, followed by a slight increase through 2007 (Figure 5c). A similar trend was seen for percent visual obscurity within 0.3m of the ground (Figure 5d). Within-year percent basal vegetation increased slightly, by ~1 unit, for each 2km from the burn perimeter (Appendix 2 Table 6). Visual obscurity also

increased slightly with distance, by 3 units for each 2km from the burn perimeter, but this effect was only marginally significant ($p = 0.052$). Fire severity showed an additional small, but statistically significant, association with visual obscurity, as percent obscurity increased 5 units for each 1 unit increase in fire severity. The distance and fire severity effects on basal vegetation and obscurity are likely driven by cover of woody species. Both basal vegetation and obscurity were positively correlated with *Lotus scoparius* cover in 2005 (Spearman's rho = 0.37 and 0.70, respectively, $p \leq 0.045$) and percent woody cover in 2007 (Spearman's rho = 0.50 and 0.41, respectively, $p \leq 0.023$). Woody cover also increased with distance as shown above. Similarly, obscurity was positively correlated with *Quercus berberidifolia* cover in 2006 (Spearman's rho = 0.40, $p \leq 0.029$), which was positively correlated with fire severity.

Rodents

As expected, fire had a strong influence on community composition, though composition varied through time on both burned and unburned plots. Dulzura kangaroo rats (*Dipodomys simulans*) were widespread among burned plots but uncommon among unburned (Figure 6). Conversely, the big-eared woodrat (*Neotoma macrotis*) was common among unburned plots in the last two spring sessions but rare among burned plots. In terms of relative abundance, unburned plots, as a group, were dominated primarily by the California mouse (*Peromyscus californicus*), although the California pocket mouse (*Chaetodipus californicus*) increased in the last two spring samples (Figure 7). In contrast, burned plots were dominated the deer mouse (*Peromyscus maniculatus*) in the first post-fire spring sample with *Dipodomys simulans* increasing in dominance over time.

Chaetodipus californicus (CHCA)

Over the entire course of the study, *Chaetodipus californicus* (CHCA) was trapped in at least one session on 100% of unburned plots and 87% of burned plots. CHCA abundance was generally low on all plots throughout the study, but ranged from 0-20 individuals on unburned plots (median = 3) and 0-16 on burned plots (median = 1). Over time, CHCA abundance increased on both unburned and burned plots, but the rate of increase was higher on unburned versus burned plots (3.6% vs. 1.3% per month, respectively; Figure 8a; Appendix 2 Table 7). At 28 months post-fire, expected abundance was, on average, 62% higher on unburned plots compared to burned plots. These results indicate CHCA are gradually recovering in burned areas, but the overall recovery rate has been relatively slow.

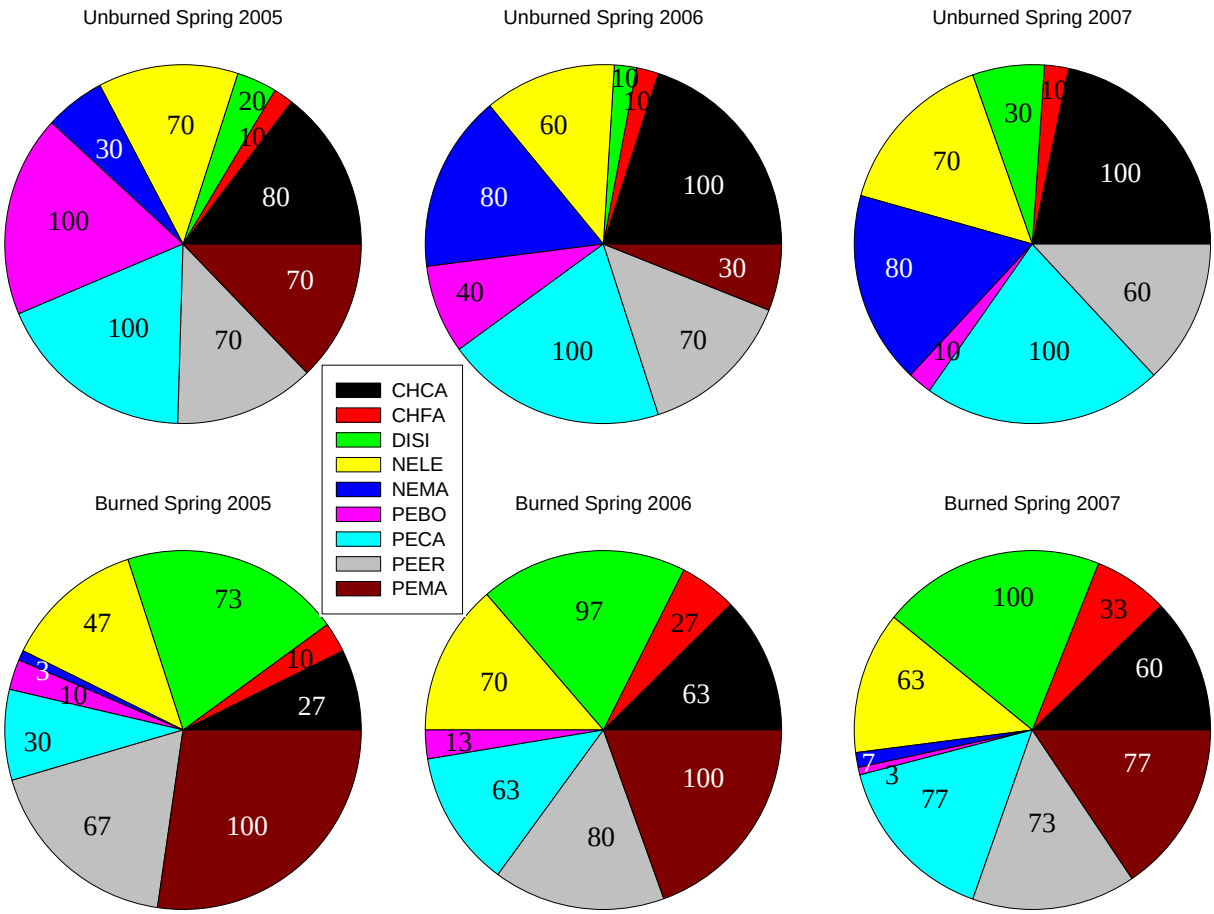

Figure 6. Relative occupancy by species during spring trapping sessions in Cleveland National Forest. Occupancy was based on minimum number of individuals known alive; numbers represent the percent of plots occupied within a type. CHFA = *Chaetodipus californicus*, CHFA = *Chaetodipus fallax* , DISI = *Dipodomys simulans*, NELE = *Neotoma lepida*, NEMA = *Neotoma macrotus*, PEBO = *Peromyscus boylii*, PECA = *Peromyscus californicus*, PEER = *Peromyscus eremicus*, PEMA= *Peromyscus maniculatus*.

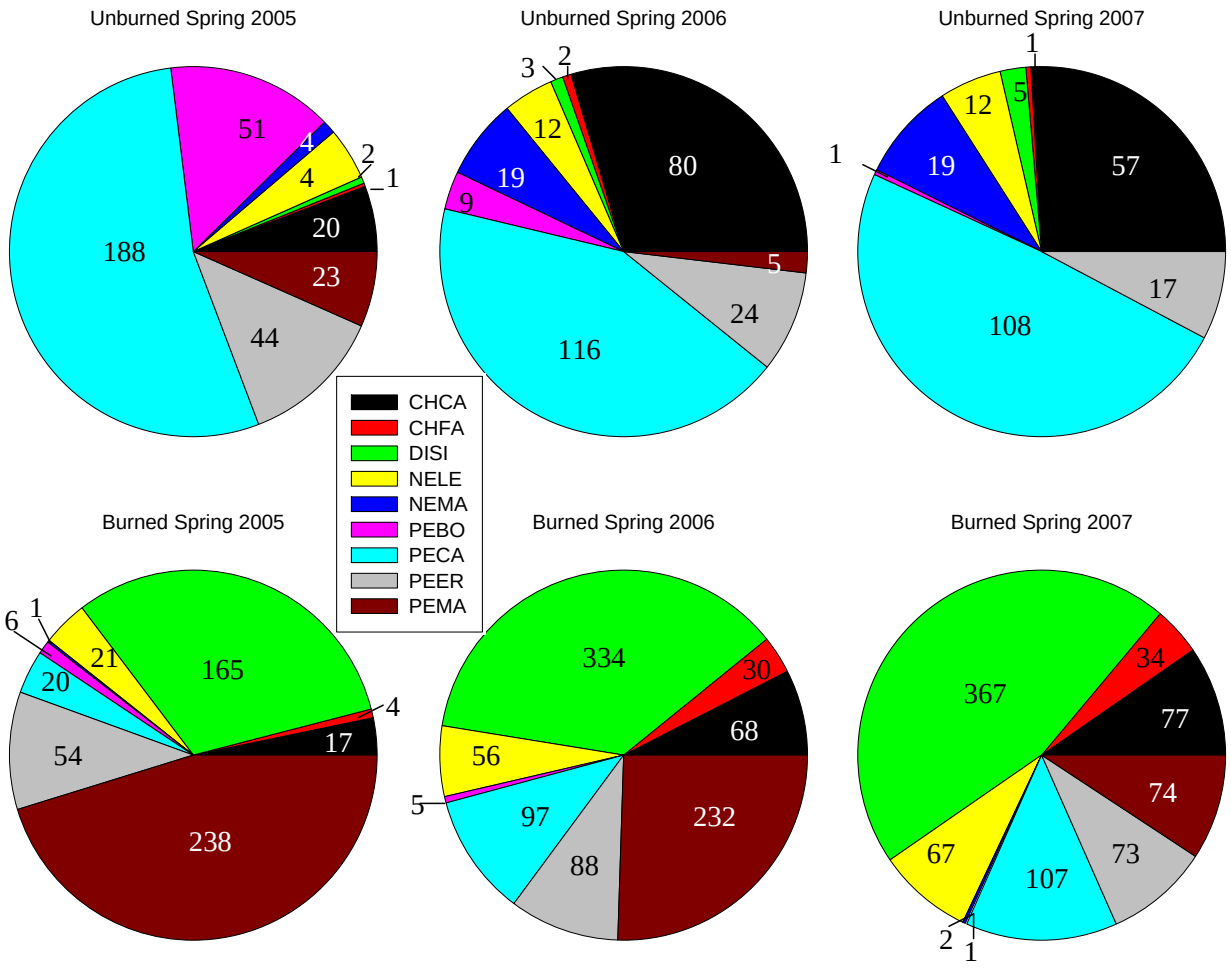

Figure 7. Relative abundance of species during spring trapping sessions in Cleveland National Forest. Abundance was based on minimum number of individuals known alive (numbers) pooled across all plots within a type. CHFA = *Chaetodipus californicus*, CHFA = *Chaetodipus fallax* , DISI = *Dipodomys simulans*, NELE = *Neotoma lepida*, NEMA = *Neotoma macrotus*, PEBO = *Peromyscus boylii*, PECA = *Peromyscus californicus*, PEER = *Peromyscus eremicus*, PEMA= *Peromyscus maniculatus*.

Across all plots, CHCA abundance also increased by 1.4% for each 1 unit increase in 2005 percent herb cover (Figure 8b), indicating bottom-up effects on CHCA abundance. While woody cover differed substantially between burn conditions in 2005 and beyond and likely influenced CHCA abundance to some extent, 2005 woody cover did not show a significant effect on expected abundance in the presence of burn, indicating the burn effect was stronger overall.

Among burned plots only, patterns of CHCA abundance were related to vegetation structure and distance from the fire perimeter. Expected CHCA abundance at 28 months post-fire increased by 2.4% with every unit increase in 2005 percent herb cover (Figure 8c; Appendix 2 Table 7). While herb cover increased with fire severity and decreased with distance from the fire perimeter, neither fire severity nor distance showed an independent effects on abundance at 28 months. However, plots farther from the perimeter added a slightly higher percentage of individuals to the population over time, though the effect appeared largely driven by plots in the midrange of distances (Figure 8d).

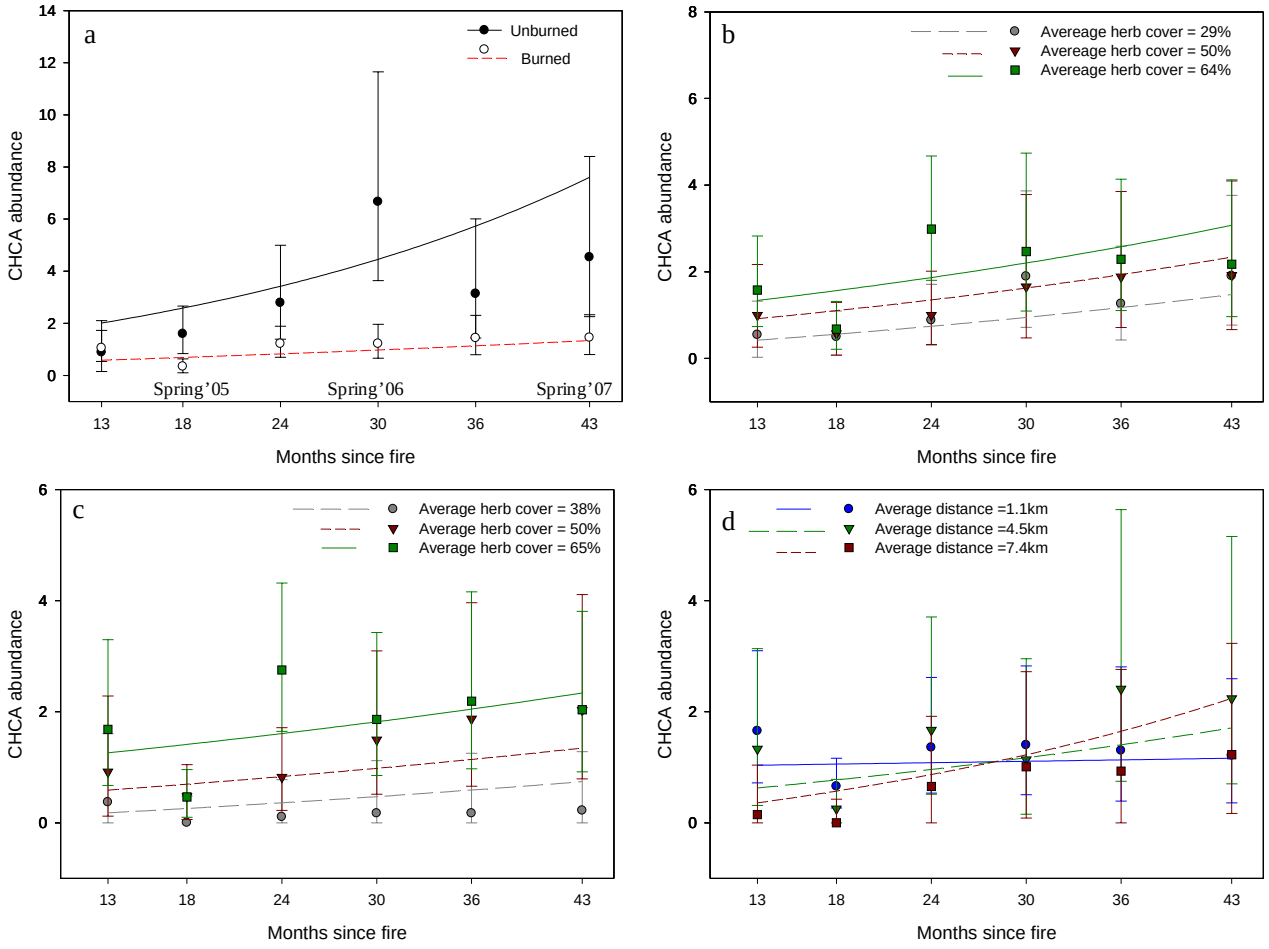

Figure 8. *Chaetodipus californicus* (CHCA) abundance over time as a function of burn status, 2005 herb cover, or distance from the fire perimeter. (a) Abundance by burn status. (b) Abundance by 2005 herb cover class on burned and unburned plots combined. (c) Abundance by 2005 herb cover class on burned plots only. (d) Abundance by distance class on burned plots only. In all graphs points represent within-year and within-class averages and bars represent 95% confidence intervals based on back-transformation of log values. Lines represent back-transformed expected values based on statistical models, with all other variables in the model held constant at their grand mean. Points and their intervals are shown primarily to give the viewer a sense of the location and spread of data within each class, rather than as formal tests of differences in the means. Note average abundance does not necessarily differ significantly among herb or distance classes because they are based on categorization of continuous variables and thus are not highly distinct groupings. However, models supported an incremental change in abundance, or its slope over time, with an incremental change in herb cover or distance as shown.

Chaetodipus fallax (CHFA)

Chaetodipus fallax (CHFA) was nearly equally uncommon among burned and unburned plots. CHFA was trapped at least once on 40% of unburned plots and 50% of burned plots. CHFA abundance was lower than CHCA, ranging from 0-2 individuals on unburned plots and 0-8 on burned plots. Low occupancy (i.e., 4 plots) combined with the restricted range of abundance values on burned plots complicated statistical comparisons of abundance between burn conditions. Abundance analyses were performed among burned plots, using those plots where CHFA were known to occur at some time during the study, to determine if CHFA was increasing in burned areas, though uncommon in unburned. Among those plots CHFA abundance increased

by 1.5% per month post-fire, but neither expected abundance nor the rate of increase were significantly related to fire severity, distance, or vegetation cover (Appendix Table 8).

Dipodomys simulans (DISI)

Dipodomys simulans (DISI) was generally more common among and more abundant on burned plots. DISI was trapped at least once on 100% of burned plots but only 50% of unburned plots. Throughout the study period DISI abundance ranged from 0-3 (median = 0) individuals on unburned plots and 0-10 on burned plots (median = 8). In addition to burn condition, abundance varied as a function of time and vegetation characteristics (Appendix 2 Table 9). On both unburned and burned plots DISI abundance increased over time, but the unburned plots increased by an average of 1.7% per month while burned plots increased and average of 3.8% per month. At 28 months post-fire expected abundance was very low on unburned plots but 17 times higher, on average, on burned plots (Figure 9a). Abundance at 28 months also increased by 1.5% for every unit increase in percent woody cover and decreased by 1.3% for every unit increase in percent herb cover. Even though abundance was lower where herb cover was high, individuals appeared to be added at slightly higher rates where herb cover was higher.

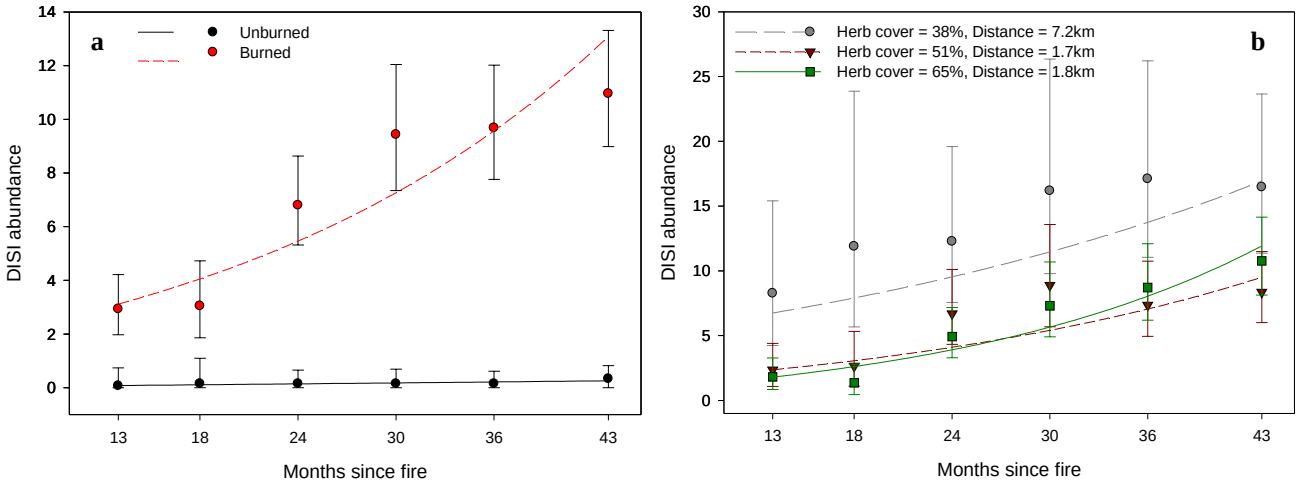

Figure 9. *Dipodomys simulans* (DISI) abundance over time as a function of (a) burn status or (b) 2005 herb cover and distance from the fire perimeter on burned plots only. In all graphs points represent within-class (i.e., burn status or herb-distance class) and within-year average abundance and bars represent 95% confidence intervals based on back-transformation of log values. Lines represent back-transformed expected values based on statistical models. Although average abundance does not necessarily differ significantly among herb-distance classes, because they are not highly distinct groupings, models supported an incremental increase in abundance with incremental increases in distance and incremental increases in the slope with increases in herb cover. In graph b, herb cover and distance are negatively correlated, but have independent effects on abundance. Model lines are based on the cover and distance values shown, which correspond to average values within each class. When distance is held constant (red and green lines), the effect of herb cover on the slope is most apparent.

Among burned plots only, expected DISI abundance at 28 months post-fire increased by 13% with every kilometer in distance away from the burn perimeter (Figure 9b; Appendix 2 Table 9). Holding distance constant, expected abundance showed little relation to herb or woody cover (e.g. bottom two lines on Figure 9b). Thus, the previously described influence of woody cover and herb cover on DISI abundance at 28 months may have been an artifact driven by distance or other associated factors, since woody cover increased and herbaceous cover

decreased with distance. However, distance alone explained only 2% of the variance in expected abundance among burned plots, indicating a small effect overall. Although expected abundance at 28 months was not significantly related to vegetation characters, the rate of increase in DISI abundance over time still increased with herb cover (Figure 9b; e.g. compare slope of bottom two lines where distance is relatively constant). While herb cover increased with fire severity, fire severity showed little independent effect on DISI abundance.

Neotoma lepida (NELE)

Overall, *Neotoma lepida* (NELE) was commonly present in both burn conditions, though not necessarily abundant. Over the course of the study, NELE was trapped at least once on 90% of unburned plots and 83% of burned plots, while abundance ranged from 0-9 individuals on unburned plots and 0-10 on burned plots (grand median = 1). Average expected log abundance at 28 months post-fire did not vary between burn conditions, but trends over time did (Appendix 2 Table 10). Average NELE abundance remained relatively constant through time among unburned plots, but increased by ~3% per month on average on burned plots (Figure 10). Among burned plots, expected abundance at 28 months and trends over time showed significant variation. But that variation was not well explained by fire severity, distance, or vegetation cover.

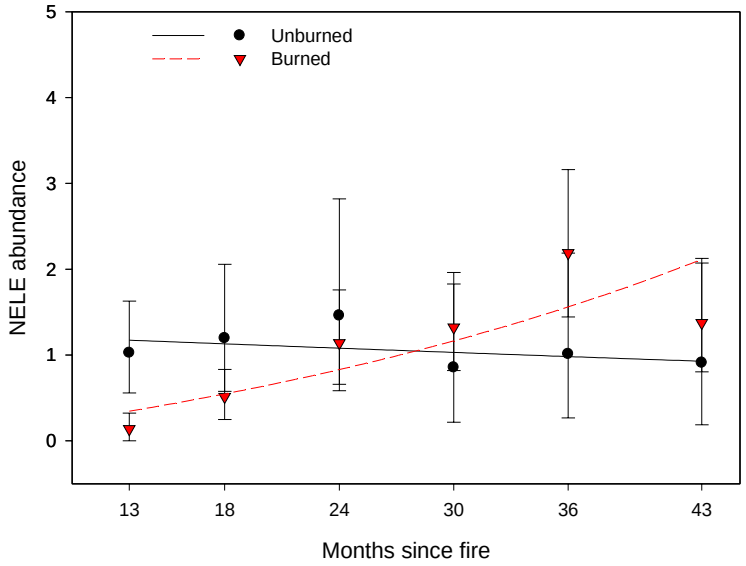

Figure 10. *Neotoma lepida* (NELE) abundance over time on burned and unburned plots. Points represent within-burn condition and within-year averages and bars represent 95% confidence intervals based on back-transformation of log values. Lines represent back-transformed expected values based on statistical models. Although average abundance does not necessarily differ significantly between burn conditions in all years, models supported a difference in the slope between conditions.

Neotoma macrotis (NEMA)

Neotoma macrotis (NEMA) was trapped at least once on 100% of unburned plots but only 20% of burned plots. NEMA abundance ranged from 0-5 individuals on unburned plots (median = 1) and 0-1 on burned plots (median = 0).Such numbers make statistical comparisons between burned and unburned plots, as well as trends in abundance on burned plots, difficult, but

they also appear unnecessary. While NEMA appears more likely to occur in unburned chaparral compared to habitat burned within 2.5 yrs, it was found in burned habitat as early as 13 months post-fire.

Peromyscus boylii (PEBO)

Peromyscus boylii (PEBO) was trapped at least once on 100% of unburned plots but only 30% of burned plots. PEBO abundance ranged from 0-10 individuals on unburned plots (median = 1) and 0-3 on burned plots (median = 0). Again statistical comparisons are difficult, but PEBO is clearly more likely to occur in unburned vs. recently burned chaparral. PEBO was found in burned habitat 18 months after fire, but there was no obvious increase in abundance through 40 months post-fire.

Peromyscus californicus (PECA)

Peromyscus californicus (PECA) was found in both burned and unburned habitat, but was far more abundant on unburned plots. PECA was trapped at least once during the study on 100% of unburned plots and 87% of burned plots. Throughout the study, PECA abundance ranged from 1-27 individuals on unburned plots (median = 10.5) and 0-15 on burned plots (median = 0). On unburned plots, abundance was highly variable through time and did not show an overall linear increase or decrease (Figure 11a). On burned plots abundance started low and increased 4% per month. At 28 months post fire average expected abundance on burned plots was still 80% lower than unburned plots (Appendix 2 Table 11).

Among burned plots, expected log abundance at 28 months post fire varied as a function of fire severity, distance, and woody cover (Appendix 2 Table 11). Holding other variables constant, abundance at 28 months increased by 39% per unit increase in fire severity (Figure 11b). Abundance at 28 months decreased by 8% with each kilometer away from the fire perimeter and increased by 1.6% for every unit increase in percent woody cover (Figure 11c). Overall, fire severity had the strongest influence as it alone explained 18% of the variability among plots, while adding distance and woody cover increased the variance explained by only ~3%. Fire severity also influenced the rate at which abundance increased over time with higher fire severity plots adding a greater proportion of individuals.

Peromyscus eremicus (PEER)

Peromyscus eremicus (PEER) was trapped at least once on 90% of unburned plots and 100% of burned plots. PEER abundance ranged from 0-17 individuals on unburned plots (median = 2) and 0-14 on burned plots (median = 2.5). Trends in log PEER abundance varied among plots, but showed no systematic increase or decrease over time on burned or unburned plots. Similarly, we found no significant differences in abundance between burned and unburned plots at any time during the study, and abundance did not appear to vary as a function of vegetation cover. Among burned plots we found no significant influence of fire severity, distance, or vegetation cover.

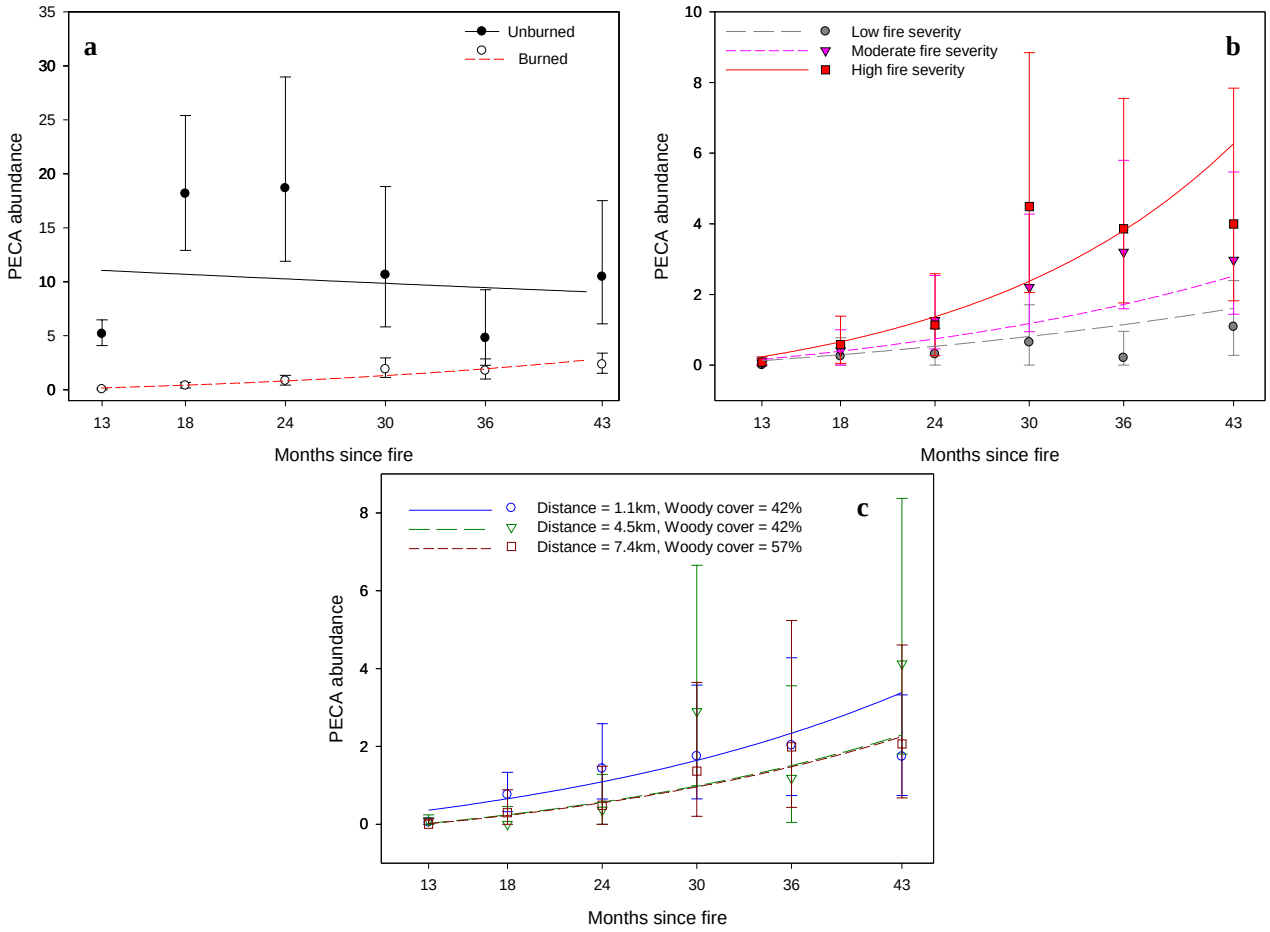

Figure 11. *Peromyscus californicus* (PECA) abundance over time as a function of (a) burn status, (b) fire severity on burned plots, or (c) 2005 woody cover and distance from the fire perimeter on burned plots. In all graphs points represent within-class (i.e., burn status or cover-distance class) and within-year average abundance and bars represent 95% confidence intervals based on back-transformation of log values. Lines represent back-transformed expected values based on statistical models. In graph b, model lines are based on holding distance and woody cover constant at their respective means. In graph c, fire severity is held constant at its mean, and model lines are based on the distance and woody cover values shown. Distance and woody cover are correlated, but have independent and opposing effects on abundance. When woody cover is held constant (blue and green lines), the distance effect is apparent. When both woody cover and distance vary (red and green lines), their independent effects may be obscured.

Peromyscus maniculatus (PEMA)

Peromyscus maniculatus (PEMA) was present in burned and unburned habitat, but abundance was generally higher among burned plots and was also influenced by vegetation structure. PEMA was trapped at least once on 90% of unburned and 100% of burned plots. PEMA abundance ranged from 0-9 individuals on unburned plots (median = 0) and 0-27 on burned plots (median = 4). Over the course of the study PEMA abundance decreased on all plots by an average of 2% per month (Appendix 2 Table 12). However, expected abundance at 28 months post fire was 4 times higher on burned than unburned plots (Figure 13a). On burned and unburned plots combined, abundance decreased slightly (by <1%) with each unit increase in percent herb cover, but herb cover explained only 3% additional variability among plots over

burn condition alone. Among burned plots only, abundance decreased by 1.5% with each unit increase in percent herb cover (Figure 13b), suggesting herb cover influenced PEMA abundance more on burned versus unburned plots. Fire severity, distance, and woody cover showed little influence on PEMA abundance among burned plots.

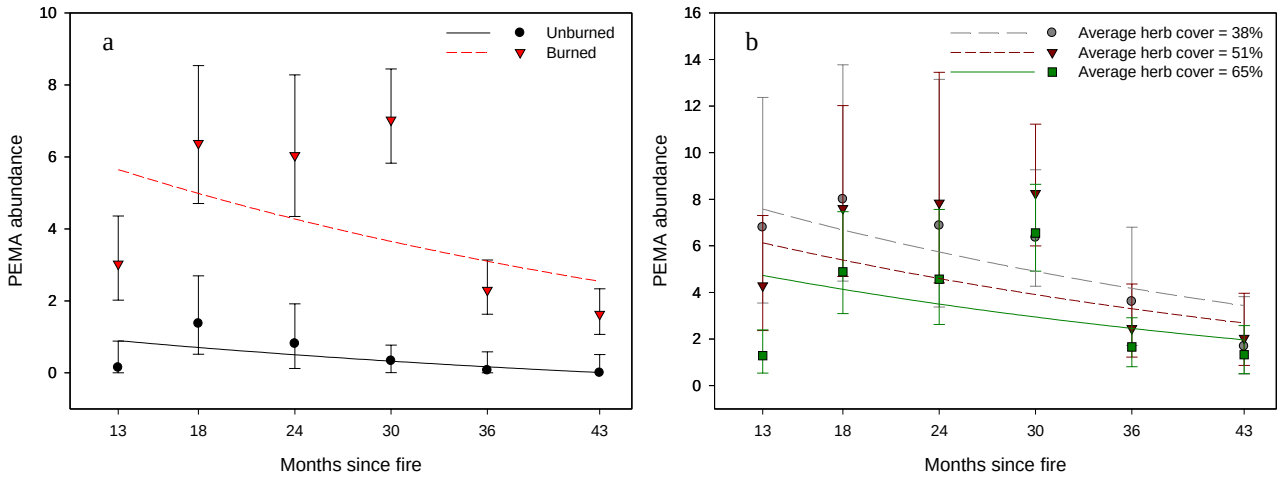

Figure 12. *Peromyscus maniculatus* (PEMA) abundance over time. (a) Abundance by burn status. (b) Abundance by 2005 herb cover on burned plots. In all graphs points represent within-class (i.e., burn status or cover class) and within-year averages and bars represent 95% confidence intervals based on back-transformation of log values. Lines represent back-transformed expected values based on statistical models. In graph b, model lines are based on holding distance and woody cover constant at their respective means.

Discussion

Our preliminary results highlight the dramatic effect fire has on rodent species composition in chaparral. As expected, burned plots were dominated by species favoring disturbed or open habitat, including deer mice (*Peromyscus maniculatus*) and Dulzura kangaroo rats (*Dipodomys simulans*), while unburned plots were dominated by species associated with mature chaparral, such as California mice (*Peromyscus californicus*).. Patterns of post-fire change in the rodent community were highly species-specific, and may include interactions between species as well as other factors, in addition to post-fire vegetation changes, that we have not yet analyzed.

Compositional differences persisted for nearly 4 years after fire, but indications of recovery, or change toward unburned conditions, are apparent in trends of individual rodent species abundance. Both *Peromyscus californicus* and *Chaetodipus californicus* showed slow, but steady increases in abundance approaching that seen in unburned chaparral. Even woodrats showed some signs of recovery, though their numbers are generally low among all plots. Some species apparently favored by the early post-fire environment, such as *Peromyscus maniculatus* showed a decline in abundance toward unburned levels several years following fire. *Dipodomys simulans*, on the other hand appeared to still be increasing in abundance 43 months post-fire, although the population increase may be slowing. Quite likely the species will persist in the community for some time. We did not find clear signs that any chaparral-associated species were not recovering, but several were too rare to rigorously evaluate.

Though we observed some effects of fire severity and distance from the fire perimeter on patterns of distribution and abundance for some species, these effects were not particularly strong and were not always in the direction expected. This may be indicative of the indirect nature of such effects, especially for fire severity. Other than its potential direct impact on mortality, which may have been more evident immediately after the fire and prior to our first survey, the effect of fire severity on rodents is likely mediated through its impact on post-fire vegetation. Indeed, our results show rodents respond to vegetation characteristics that, in turn, were affected by fire severity. Rodents often showed greater response to herbaceous cover than to cover of the dominant shrubs. This may be because herb cover showed greater variation through time than shrub cover, rendering the effect easier to capture statistically. But it probably also reflects the importance of herbs and their seeds as food sources for many rodent species. Thus, variation in herb abundance over time can substantially influence post-fire recovery of mammal communities. This may be especially important in dry years when resources are scarce.

Despite the potential importance of herbs in the post-fire environment, it must be emphasized that nonnative cover was relatively low on our chaparral plots, and native shrubs were recovering well. In shrublands where nonnative herbs are more abundant, due for example to short fire-return intervals, different results are likely. We will further explore this issue using data from our study plots at Rancho Jamul Ecological Reserve, which span a range of pre-fire disturbance histories and invasion by exotic annuals.

Appendix 1: An Explanation of HLM

A brief, didactic background of HLM is provided here in order to aid understanding of the analyses. For a detailed and highly readable exposition, readers are referred to Raudenbush and Bryk (2002).

HLM is a powerful statistical technique allowing regression-style analysis of data with a nested, or hierarchical, structure. Such data are not properly analyzed using standard Ordinary Least Squares (OLS) regression due to violation of the independent observations assumption, which can lead to biased estimation of standard errors and significance tests. HLM employs a multi-level, mixed effects model structure to explicitly account for hierarchical nesting of data. More importantly, though, the model structure allows the analyst to explore whether relationships examined within lower hierarchical levels (e.g. within plots) are moderated by factors that vary across higher level units (e.g. among plots).

An illustrative, but oversimplified, example using species abundance as a response variable may initially aid understanding. To begin, if we wanted to know whether and how abundance changed on plots over time, we could plot abundance against time separately for each of our 40 plots. We might see that abundance seems to increase on several plots, stays relatively constant on others, and maybe even decreases on a few. If we quantified these relationships using standard regression equations (abundance = $\beta_0 + \beta_1$*X; where β_0 is the intercept, β_1 is the slope, and X is time), we could then determine the average "trend" in abundance over time using the average of the slope estimates (the rate of increase or decrease in abundance over time). We could also test whether the variability in the set of 40 slope estimates (or coefficients) was statistically different from 0. Even if the average slope is near zero (no trend), when there is significant variability among plots it makes sense to look for variables that explain differences in the slopes among plots. These could include burn variables or distance (e.g. burned plots may have steeper slopes, or higher rates of increase in abundance, than unburned plots).

In addition to examining slopes, we can also examine the intercepts of the relationship, or the expected value of abundance when time = 0. If time is scaled so that a value of 0 represents trapping session 1, or some other session of interest, this actually makes some sense. As with the slope, we can determine whether there is significant variability among the 40 expected values for abundance at session 1 and whether this variability is explained by burn severity or distance variables (e.g. unburned plots may have higher abundance at Session 1 than burned plots). While the intercept technically represents a value of the response variable at a specific value of the explanatory variable, if there is no difference in the slope between two conditions one can infer that the difference in the intercept applies to other values of the explanatory variable in a constant fashion. For example, if the is no difference in Session 1 abundance between burned and unburned plots and no difference in slopes between burn conditions, one can infer that abundance never differs substantially between burned and unburned plots. If the slopes do differ, difference may emerge in later sessions even if they are not detected at session 1.

While the example above illustrates the approximate logic of HLM, the procedure is much more statistically efficient and more complex than implied. A slightly more mathematical explanation will aid interpretation of the statistical tables accompanying each analysis. Essentially, HLM expands the traditional linear regression equation so that each "β" is actually represented by its own regression equation. That is:

1. $Y = \beta_{0j} + \beta_{1j}*X + r_{ij}$, where

2. $\beta_{0j} = \gamma_{00} + u_{0j}$, and
3. $\beta_{1j} = \gamma_{10} + u_{1j}$.

Equation 1 is applied to each individual plot (denoted by the subscript "j"), and X is a variable that varies within plots (e.g. time), while "r_{ij}" represents unexplained variation in Y within plots. Each β_n is a "random plot effect." That is, each β_{nj} is a function of a "fixed" effect (γ_{q0}; essentially the average coefficient across plots) plus random variation among plots (u_{qj}; effectively the variability in the coefficients among plots).

Rather than being completely random, the variation in each plot effect (β_{0j}, β_{1j},… β_{nj}) may depend in part on some plot-level variable, W, which varies among plots (e.g. 2003 burn condition, fire severity, etc). This yields the following modified equations:

4. $\beta_{0j} = \gamma_{00} + \gamma_{01}*W_j + u_{0j}$, and
5. $\beta_{1j} = \gamma_{10} + \gamma_{11}*W_j + u_{1j}$.

In equation 4, γ_{00} is the value of the intercept, β_0, when W = 0; and γ_{01} is the incremental change in β_0 for each one unit change in W. Similarly, in equation 5 γ_{10} is the value of the slope, β_1, when W = 0; and γ_{11} is the incremental change in β_1 for each one unit change in W.

Recalling our abundance example, let W represent 2003 burn condition with a value of 0 representing unburned and a value of 1 representing burned. To determine whether expected abundance at session 1 differs between burned and unburned plots, one examines the coefficient for W, γ_{01}. When W = 0, $\beta_0 = \gamma_{00}$ and the expected average abundance for unburned plots. When W = 1, β_0 increases (or decreases) by an amount = γ_{01} giving the average expected abundance for burned plots. Similarly, we can examine how 2003 burn condition affects the rate of change in richness, or the slope β_1. In the case of the slope, this is often referred to as a "cross-level interaction" effect, i.e., a factor differing among plots moderates the relationship between X and Y within plots.

In HLM all the coefficients in the various equations described above are estimated simultaneously using maximum likelihood algorithms. Nonetheless, the modeling process usually occurs in 3 main steps. Within each of the three steps, the primary goals are to (a) estimate and test significance of the fixed effects (i.e., slopes and intercepts, γ_{qn}); (b) estimate and test the amount of variability among plots in the slopes and intercepts ("random effects" u_{nj}); and (c) estimate the amount of variability in the random effects explained by the fixed effects, which is conceptually similar to R^2 in OLS regression. Fixed effects are tested individually using t-ratios, as in OLS regression, and random effects are tested using a χ^2 statistic.

Step1, the "unconditional model," is a model with no predictors (X's or W's). In step 1, we estimate the within-plot variability in Y (r_{ij}) along with the grand mean (γ_{00}) and variability in within plot means (u_{0j}). In Step 2, the "random coefficients model", we estimate the overall, or average, relation ship between X and Y (γ_{10}, the fixed slope coefficient), the average expected value of Y when X = 0 (γ_{00}, the fixed within plot intercept coefficient), and how much of the within plot variation in Y is explained by X by examining the reduction in r_{ij} compared to Step1. We also estimate how much random variation exists among plots in the X-Y relationship (u_{1j}; or variation in the slope coefficient) and the value when X = 0 (u_{0j}; or variation in the within plot intercept coefficient). If the variation among plots for either coefficient is not significantly different than zero, the effect may be specified as completely fixed (i.e., equal across plots with no variation). When the variation is significant, one can examine the extent to which this

variation depends on one or more group level variables in step 3, the "coefficients as outcomes model." Thus, in step 3 we estimate the effect of W on the within plot slope or intercept (γ_{11} or γ_{01} , respectively). We also estimate how much of the variation in those coefficients among plots is explained by W by examining the reduction in u_{1j} or u_{0j} compared to step 2. We can also examine whether the remaining variation is significantly different from 0.

In the simple example above, the intercept for the within plot relationship between time and abundance ($ß_{0j}$) was set to equal the first trapping session by assigning time = 0 to that session and representing the following sessions as months since session 1. If desired, the intercept can be made to represent other points in time by rescaling the time variable. Sometimes, such as when modeling nonlinear trends over time, this is statistically necessary. Rescaling of the time variable is a simple linear transformation. One chooses the location of 0 by subtracting a specific, constant value from each value for time (e.g. subtracting 13 from the "months since fire" value corresponding to each trapping session). This linear transformation has no effect on the estimation and interpretation of the linear slope coefficient for time. However, when nonlinear trends are present, the estimation and interpretation of coefficients depend on time scaling since the slope is not constant. In these cases, the intercept coefficient for time (γ_{10}) represents the instantaneous rate of change at time = 0, while the intercept coefficient for time^2 (γ_{20}) represents acceleration or deceleration in the rate of change.

Appendix 2: HLM Tables

Table 1. HLM models for density of woody adults or seedlings in $20m^2$ on burned plots.

Adult density	***Model 1: Unconditional***			***Model 2: Random coefficients***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log density ($ß_0$)						
Intercept (γ_{00})	4.974	0.049	29***	5.246	0.058	29***
For Time slope ($ß_1$)						
Intercept (γ_{10})				0.021	0.002	87***
For Time^2 slope ($ß_2$)						
Intercept (γ_{20})				-0.003	0.0002	87***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log density (u_{0j})	0.027	44.98	29*	0.066	222.98	29***
Within plot variability r_{ij}	0.147			0.030		
Proportion of within plot variance explained by time				*0.80*		

Seedling density	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log density($ß_0$)									
Intercept (γ_{00})	4.479	0.121	29***	4.851	0.125	29***	5.192	0.189	28***
Distance (γ_{01})							-0.093	0.042	28*
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.031	0.004	29***	-0.046	0.006	28***
Distance (γ_{11})							0.004	0.001	28**
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log density (u_{0j})	0.383	176.73	29***	0.443	317.88	29***	0.392	275.05	28***
Proportion of variance in seedling density explained							*0.11*		
Time slope (u_{1j})				0.00025	67.80	29***	0.00013	47.12	28*
Proportion of variance in rate of change explained							*0.48*		
Within plot variability r_{ij}	0.225			0.053					
Proportion of within plot variance explained by time				*0.76*					

Notes: The dependent variables are started-log transformed from their original metrics. In the model for adult density, time is scaled so a value of zero represents the 2006 sample. For seedling density, a 0 value of time represents 2005. *p≤0.05; **p≤0.01; ***p≤0.001

Table 2. HLM models for woody canopy cover (%) and height (m) on burned plots.

Woody cover	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average woody cover ($ß_0$)									
Intercept (γ_{00})	56.622	1.648	29***	61.933	1.952	29***	56.997	2.646	28***
Distance (γ_{01})							1.341	0.562	28*
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.661	0.072	87***	0.661	0.072	86***
For Time^2 slope ($ß_2$)									
Intercept (γ_{20})				-0.055	0.008	87***	-0.055	0.008	86***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average woody cover (u_{0j})	44.967	62.16	29**	72.608	209.27	29***	61.363	175.10	28***
Proportion of variance in average woody cover explained							*0.15*		
Within plot variability r_{ij}	117.967			35.042					
Proportion of within plot variance explained by time				*0.70*					
Woody canopy height	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average woody height ($ß_0$)									
Intercept (γ_{00})	0.553	0.019	29***	0.502	0.018	29***	0.397	0.041	28***
Fire severity (γ_{01})							0.055	0.020	28**
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.004	0.000	88***	0.004	0.000	87***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average height (u_{0j})	0.010	250.27	29***	0.011	708.76	29***	0.009	583.25	28***
Proportion of variance in woody height explained							*0.15*		
Within plot variability r_{ij}	0.004			0.001					
Proportion of within plot variance explained by time				*0.65*					

Notes: For woody cover, time is scaled so a value of zero represents the 2006 sample. For height, a 0 value of time represents 2005. *p≤0.05; **p≤0.01; ***p≤0.001

Table 3. HLM model for herb canopy cover (%) on burned plots.

Herb cover	*Model 1: Unconditional*			*Model 2: Random coefficients*			*Model 3: Coefficients-as-outcomes*		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average herb cover ($ß_0$)									
Intercept (γ_{00})	28.156	1.646	29***	19.100	1.885	29***	6.749	6.016	27.000
Fire severity (γ_{01})							3.468	1.051	27**
Distance (γ_{02})							-1.491	0.477	27**
For Time slope ($ß_1$)									
Intercept (γ_{10})				-1.785	0.075	87***	-1.785	0.075	85***
For Time^2 slope ($ß_2$)									
Intercept (γ_{20})				0.094	0.007	87***	0.094	0.007	85***
Random Effects	**Variance**	**χ2**	**df**	**Variance**	**χ2**	**df**	**Variance**	**χ2**	**df**
Average herb cover (u_{0j})	0.181	0.18	29.000	71.748	198.01	29***	48.562	133.50	27***
Proportion of variance in average herb cover explained							*0.32*		
Within plot variability r_{ij}	456.901			36.934					
Proportion of within plot variance explained by time				*0.92*					

Notes: Time is scaled so a value of zero represents the 2006 sample *p≤0.05; **p≤0.01; ***p≤0.001

Table 4. HLM model for nonnative herb canopy cover (%) on burned plots.

Nonnative herb cover	*Model 1: Unconditional*			*Model 2: Random coefficients*			*Model 3: Coefficients-as-outcomes*		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log cover ($ß_0$)									
Intercept (γ_{00})	2.000	0.153	29***	2.383	0.147	29***	2.883	0.203	28***
Distance (γ_{01})							-0.136	0.048	28**
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.032	0.007	29***	-0.116	0.037	28**
Fire severity (γ_{11})							0.016	0.007	28*
Random Effects	**Variance**	**χ2**	**df**	**Variance**	**χ2**	**df**	**Variance**	**χ2**	**df**
Average log cover (u_{0j})	0.576	138.35	29***	0.494	198.01	29***	0.384	90.77	28***
Proportion of variance in average log cover explained							*0.22*		
Time slope (u_{1j})				0.001		29***	0.001	54.18	28**
Proportion of variance in rate of change explained							*0.14*		
Within plot variability r_{ij}	0.459			0.207					
Proportion of within plot variance explained by time				*0.55*					

Notes: The dependent variable is started-log transformed from its original metric. Time is scaled so a value of zero represents the 2005 sample *p≤0.05; **p≤0.01; ***p≤0.001

Table 5. HLM models for log native herb canopy cover (%) on burned plots.

Log native annual cover	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log cover ($ß_0$)									
Intercept (γ_{00})	1.884	0.065	29***	1.564	0.112	29***	1.715	0.130	28***
Distance (γ_{01})							-0.041	0.016	28*
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.135	0.003	87***	-0.135	0.003	85***
For Time^2 slope ($ß_2$)									
Intercept (γ_{20})				0.003	0.001	29***	-0.006	0.002	28*
Fire severity (γ_{21})							0.002	0.0004	28***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log cover (u_{0j})	0.0003	5.43	29***	0.278	102.86	29***	0.245	93.31	28***
Proportion of variance in average herb cover explained							*0.12*		
Time^2 slope (u_{1j})				1.00E-05	75.01	29***	9.61E-06	63.70	28***
Proportion of variance in rate of change explained							*0.04*		
Within plot variability r_{ij}	2.079			0.109					
Proportion of within plot variance explained by time				*0.95*					

Log native perennial herb cover	***Model 1: Unconditional***			***Model 2: Random coefficients***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log cover ($ß_0$)						
Intercept (γ_{00})	1.752	0.127	29***	1.595	0.129	29***
For Time slope ($ß_1$)						
Intercept (γ_{10})				-0.033	0.005	29***
For Time^2 slope ($ß_2$)						
Intercept (γ_{20})				0.002	0.0005	87***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log cover (u_{0j})	0.385	128.97	29***	0.464	439.20	29***
Time slope (u_{1j})				0.0005	69.69	29***
Within plot variability r_{ij}	0.335			0.098		
Proportion of within plot variance explained by time				*0.71*		

Notes: The dependent variables are started-log transformed from their original metrics. Time is scaled so a value of zero represents the 2006 sample *p≤0.05; **p≤0.01; ***p≤0.001

Table 6. HLM models for basal vegetation cover (%) and vertical obscurity (5) on burned plots.

Basal vegetation	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average basal cover ($ß_0$)									
Intercept (γ_{00})	29.299	0.855	29***	19.713	0.604	29***	17.469	1.269	28***
Distance (γ_{01})							0.610	0.282	28*
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.426	0.056	87***	-0.426	0.056	86***
For Time^2 slope ($ß_2$)									
Intercept (γ_{20})				0.100	0.006	87***	0.100	0.006	86***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average basal cover (u_{0j})	0.050	19.51	29	15.095	86.71	29***	12.958	75.83	28***
Proportion of variance in average basal cover explained							*0.14*		
Within plot variability r_{ij}	101.087			22.750					
Proportion of within plot variance explained by time				*0.77*					
Obscurity	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average obscurity ($ß_0$)									
Intercept (γ_{00})	35.769	2.428	29***	27.556	2.596	29***	-4.865	11.502	27
Fire severity (γ_{01})							5.212	2.033	27*
Distance (γ_{02})							1.525	0.750	27
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.675	0.177	87***	-0.675	0.177	85***
For Time^2 slope ($ß_2$)									
Intercept (γ_{20})				0.086	0.022	87***	0.086	0.022	
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average obscurity (u_{0j})	66.066	45.38	29*	102.192	65.59	29***	82.190	54.42	27**
Proportion of variance in average obscurity explained							*0.20*		
Within plot variability r_{ij}	350.872			242.766					
Proportion of within plot variance explained by time				*0.31*					

Notes: Time is scaled so a value of zero represents the 2006 sample *p≤0.05; **p≤0.01; ***p≤0.001

Table 7. HLM model for *Chaetodipus californicus* abundance.

Burned and Unburned Plots	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	0.886	0.099	39***	0.898	0.101	39***	1.627	0.163	37***
Burn effect (γ_{01})							-0.972	0.184	37***
Herb cover (γ_{02})							0.014	0.005	37*
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.018	0.005	39***	0.035	0.010	38**
Burn effect (γ_{11})							-0.022	0.011	38
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average abundance (u_{0j})	0.347	266.94	39***	0.382	471.14	39***	0.286	344.82	37***
Proportion of variance in average abundance at 28 months explained							*0.25*		
Time slope (u_{1j})				0.001	143.81	39***	0.001	132.69	38***
Proportion of variance in rate of abundance increase explained							*0.08*		
Within plot variability r_{ij}	0.356			0.206					
Proportion of within plot abundance variance explained by time				*0.42*					
Burned Plots Only	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	0.732	0.116	29***	0.741	0.118	29***	0.741	0.101	28***
Herb cover (γ_{02})							0.024	0.008	28**
For Time slope ($ß_1$)				0.013	0.006	29*			
Intercept (γ_{10})							0.013	0.006	28*
Distance (γ_{11})							0.004	0.002	28*
Random Effect	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.369	236.68	29***	0.399	410.86	29***	0.298	304.64	28***
Proportion of variance in average abundance at 28 months explained							*0.25*		
Time slope (u_{1j})				0.001	118.43	29***	0.001	104.47	28***
Proportion of variance in rate of abundance increase explained							*0.11*		
Within plot variability r_{ij}	0.309			0.181					
Proportion of within plot abundance variance explained by time				*0.41*					

Notes: The dependent variable is started-log transformed from its original metric. Time is scaled so a value of zero represents the 28months post-fire. Herb cover is from 2005. Both herb cover and distance are scaled so a value of zero represents the grand mean. *p≤0.05; **p≤0.01; ***p≤0.001.

Table 8. HLM model for *Chaetodipus fallax* abundance.

Burned and Unburned Plots	***Model 1: Unconditional***			***Model 2: Random coefficients***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)						
Intercept (γ_{00})	0.713	0.147	14***	0.722	0.149	14***
For Time slope ($ß_1$)						
Intercept (γ_{10})				0.015	0.007	14*
Random Effects	**Variance**	**$\chi 2$**	**df**	**Variance**	**$\chi 2$**	**df**
Average log abundance (u_{0j})	0.279	104.81	14***	0.301	152.21	14***
Time slope (u_{1j})				0.0004	34.77	14**
Within plot variability r_{ij}	0.258			0.182		
Proportion of within plot abundance variance explained by time				*0.29*		

Notes: The dependent variable is started-log transformed from its original metric. Time is scaled so a value of zero represents the 28months post-fire. *p≤0.05; **p≤0.01; ***p≤0.001

Table 9. HLM model for *Dipodomys simulans* abundance.

Burned and Unburned Plots	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	1.540	0.153	39***	1.562	0.153	39***	-0.561	0.218	36*
Burn effect (γ_{01})							2.831	0.302	36***
Herb cover (γ_{02})							-0.013	0.005	36*
Woody cover (γ_{03})							0.015	0.006	36*
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.032	0.005	39***	0.017	0.007	37*
Burn effect (γ_{11})							0.021	0.008	37*
Herb cover (γ_{12})							0.001	0.0002	37**
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.899	644.18	39***	0.943	1708.44	39***	0.200	363.92	36***
Proportion of variance in average abundance at 28 months explained							*0.79*		
Time slope (u_{1j})				0.001	167.59	39***	0.0004	105.74	37***
Proportion of variance in rate of abundance increase explained							*0.43*		
Within plot variability r_{ij}	0.348			0.132					
Proportion of within plot abundance variance explained by time				*0.62*					
Burned Plots Only	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	2.003	0.112	29***	2.030	0.110	29***	2.030	0.108	28***
Distance (γ_{01})							0.125	0.030	28***
For Time slope ($ß_1$)				0.041	0.005	29***			
Intercept (γ_{10})							0.041	0.004	28***
Herb cover (γ_{11})							0.001	0.0003	28**
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.316	156.10	29***	0.350	437.53	29***	0.342	419.12	28***
Proportion of variance in average abundance at 28 months explained							*0.02*		
Time slope (u_{1j})				0.001	99.09	29***	0.0004	73.74	28***
Proportion of variance in rate of abundance increase explained							*0.33*		
Within plot variability r_{ij}	0.433			0.149					
Proportion of within plot abundance variance explained by time				*0.66*					

Notes: The dependent variable is started-log transformed from its original metric Time is scaled so a value of zero represents the 28months post-fire. Herb cover and woody cover are from 2005 and scaled so a value of zero represents the grand mean. Distance is scaled so a value of zero represents the grand mean. *p≤0.05; **p≤0.01; ***p≤0.001.

Table 10. HLM model for *Neotoma lepida* abundance.

Burned and Unburned Plots	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	0.703	0.071	39***	0.716	0.072	39***	0.716	0.072	39****
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.020	0.004	39***	-0.004	0.006	38.000
Burn effect (γ_{11})							0.032	0.007	38***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.152	150.23	39***	0.177	229.12	39***	0.177	229.08	39***
Proportion of variance in average abundance at 28 months explained									
Time slope (u_{1j})				0.00045	90.08	39***	0.00026	67.68	38**
Proportion of variance in rate of abundance increase explained							*0.42*		
Within plot variability r_{ij}	0.321			0.217					
Proportion of within plot abundance variance explained by time				*0.32*					
Burned Plots Only	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	0.695	0.078	29***	0.714	0.080	29***			
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.028	0.005	29***			
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.131	91.98	29***	0.163	156.32	29***			
Time slope (u_{1j})				0.0004	58.02	29***			
Within plot variability r_{ij}	0.362			0.222					
Proportion of within plot abundance variance explained by time				*0.39*					

Notes: The dependent variable is started-log transformed from its original metric Time is scaled so a value of zero represents the 28months post-fire. *p≤0.05; **p≤0.01; ***p≤0.001

Table 11. HLM model for *Peromyscus californicus* abundance.

Burned and Unburned Plots	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	1.134	0.138	39***	1.152	0.138	39***	2.396	0.047	38***
Burn effect (γ_{01})							-1.659	0.113	38***
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.028	0.006	39***	-0.006	0.007	38
Burn effect (γ_{11})							0.045	0.009	38***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.704	376.34	39***	0.730	618.32	39***	0.210	204.58	38***
Proportion of variance in average abundance at 28 months explained							*0.71*		
Time slope (u_{1j})				0.0008	105.19	39***	0.0005	74.98	38**
Proportion of variance in rate of abundance increase explained							*0.38*		
Within plot variability r_{ij}	0.488			0.294					
Proportion of within plot abundance variance explained by time				*0.40*					
Burned Plots Only	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	0.711	0.100	29***	0.737	0.103	29***	0.737	0.089	26***
Fire severity (γ_{01})							0.329	0.101	26**
Distance (γ_{02})							-0.085	0.025	26**
Woody cover (γ_{03})							0.016	0.005	26**
For Time slope ($ß_1$)									
Intercept (γ_{10})				0.039	0.006	29***	0.039	0.005	28***
Fire severity (γ_{11})							0.018	0.007	28*
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.226	105.77	29***	0.289	236.93	29***	0.229	187.93	26***
Proportion of variance in average abundance at 28 months explained							*0.21*		
Time slope (u_{1j})				0.001	77.42	29***	0.001	63.86	28***

Proportion of variance in rate of abundance increase explained			*0.17*
Within plot variability r_{ij}	0.511	0.240	
Proportion of within plot abundance variance explained by time		*0.53*	

Notes: The dependent variable is started-log transformed from its original metric Time is scaled so a value of zero represents the 28months post-fire. Fire severity, distance, and woody cover (from 2005) are scaled so a value of zero represents the grand mean of each variable. *p≤0.05; **p≤0.01; ***p≤0.001

Table 12. HLM model for *Peromyscus maniculatus* abundance.

Burned and Unburned Plots	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effects	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	1.280	0.105	39***	1.266	0.104	39***	0.198	0.095	37*
Burn effect (γ_{01})							1.424	0.114	37***
Herb cover (γ_{02})							-0.007	0.003	37*
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.021	0.005	39***	-0.021	0.005	39***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.364	199.80	39***	0.372	232.47	39***	0.057	65.28	37**
Proportion of variance in average abundance at 28 months explained							*0.85*		
Time slope (u_{1j})				0.0002	52.03	39	0.0002	52.06	39
Within plot variability r_{ij}	0.530			0.448					
Proportion of within plot abundance variance explained by time				*0.16*					
Burned Plots Only	***Model 1: Unconditional***			***Model 2: Random coefficients***			***Model 3: Coefficients-as-outcomes***		
Fixed Effect	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**	**Coefficient**	**SE**	**df**
For Average log abundance ($ß_0$)									
Intercept (γ_{00})	1.597	0.074	29***	1.583	0.074	29***	1.583	0.066	28***
Herb cover (γ_{02})							-0.015	0.005	28**
For Time slope ($ß_1$)									
Intercept (γ_{10})				-0.022	0.006	29***	-0.022	0.006	29***
Random Effects	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**	**Variance**	**χ^2**	**df**
Average log abundance (u_{0j})	0.073	50.39	29**	0.086	59.29	29***	0.056	47.08	28*
Proportion of variance in average abundance at 28 months explained							*0.35*		
Time slope (u_{1j})				0.0004	42.17	29	0.0004	42.17	29
Within plot variability r_{ij}	0.593			0.490					
Proportion of within plot abundance variance explained by time				*0.17*					

Notes: The dependent variable is started-log transformed from its original metric Time is scaled so a value of zero represents the 28months post-fire. Herb cover is scaled so a value of zero represents the grand mean. *p≤0.05; **p≤0.01; ***p≤0.001

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